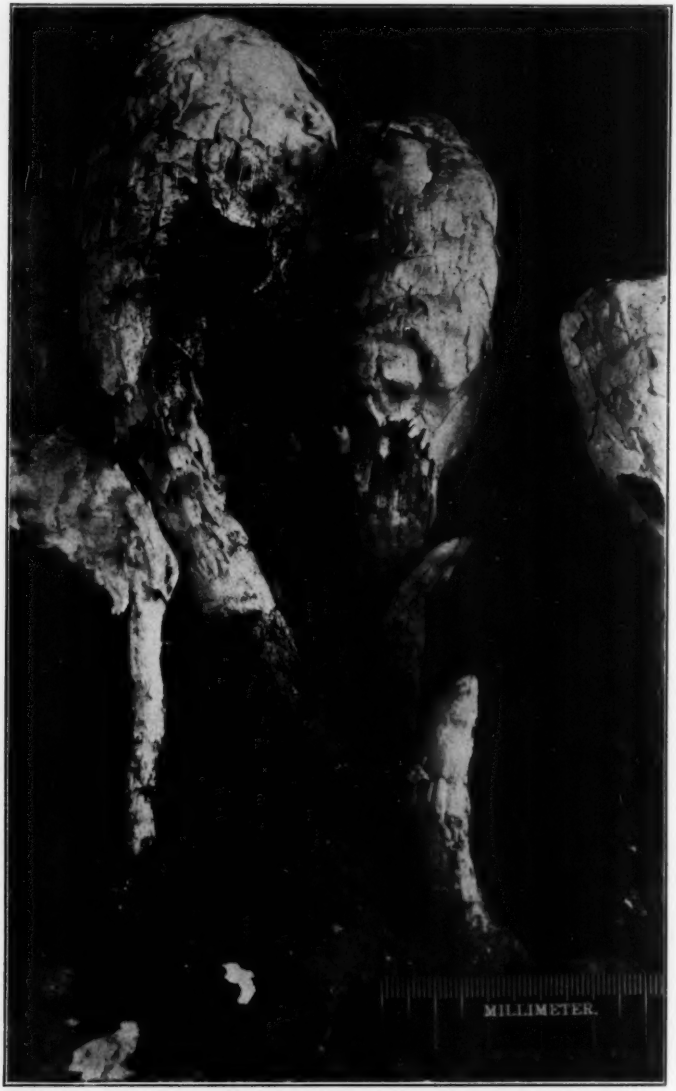

PODAXIS

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A STUDY OF THE GENUS PODAXIS[1]

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(WITH PLATES 1–12)

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INTRODUCTION

Podaxis Desv. is a generic name now applied to a peculiar fungus which occurs generally though intermittently in somewhat restricted areas in a belt encircling the earth approximately within the fortieth parallels north and south of the equator. While mature *Podaxis* has been known to botanists for over two hundred and fifty years, its life history has never been fully made out, for several reasons; among these may be named its more or less hypogeous habit and the consequent difficulty of securing young sporo-

[1] Based on an examination of North American collections, mainly Californian.

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phores. In North America there have been until recently only isolated collections and brief descriptions.

This work was started in the spring of 1929, when the writer undertook to find the fungus growing on the Colorado Desert. Many localities were visited and many inquiries made, all of which met the discouraging response, "We have never seen your plant!" Within two weeks after returning to the laboratory a packet containing three small specimens of *Podaxis* arrived from Indio, California (Smiley), with the question, "Is this the plant for which you were looking in our garden?"

Many collections came in from different places in the Colorado Desert during the three succeeding years, so that it was possible to examine several hundred specimens in a fresh state at all stages of growth.[2] This examination revealed the extraordinary variations which characterize the North American plant.

This fungus is described under such a diversity of generic and specific names, the descriptions indicating no greater variations than already had been observed in the Colorado Desert plant, that a query naturally arose as to the actual number of valid species.

The next quest was to assemble as much material as possible from various localities. Due to the generous response of officials connected with herbaria at home and abroad, also of foreign collectors, the writer was able to make some of the desired comparisons. Twelve distinct collections and reports were received from South Africa alone. There are many regions from which *Podaxis* has been reported that are not represented in our material, and we are still hoping to hear from some of these.

DESCRIPTION OF THE NORTH AMERICAN PLANT

As in other species of fungi sporophores originate from mycelium which ramifies in soil where warmth and moisture conditions meet the requirements of the plant. They may occur in rather large numbers in a sandy, adobe or semi-adobe soil, particularly after seasonal rains, in fertilized fields which are being reclaimed by irrigation, or where there is a free use of the garden hose; "never in silt (hard lands) or in alkali spots" (letter,

[2] Some plants received from Indio (2–3 mm.) could barely be distinguished from particles of soil.

Northrop). A clay river bottom in which the water dried out slowly was a favored locality in 1928 (Phoenix, Arizona, Edwards). Although this spot has been under observation, sporophores are not known to have reappeared.

Battle Creek Meadow in north central California marks the latitudinal limit of known range in the western hemisphere (two small sporophores, Jepson). The plant has been collected quite abundantly at El Centro, 65 feet below sea level, also in the Panamint Mountains in southeastern California at an elevation of five thousand feet (Hall and Chandler), indicating a wide altitudinal range.

Although *Podaxis* has been collected in every continent, Africa appears to be the center of maximum productivity; it is also found in the three groups of islands northwest of Africa.

While there are records that collections have been made in California in practically every month of the year, its active growing "season" here may be named as extending from April to October, the largest number of sporophores appearing usually in the months of May and June, or often later under the influence of the moisture supply. When the heat becomes excessive (125° F. in the shade), plants wither and cease to grow. Temperature at night during summer months is 80–90° F. (Indio, Smiley). An average day temperature in El Centro in September, 100–110° (Northrop).

Podaxis is a well developed plant while still underground, often attaining a growth up to three inches before breaking through to the surface. Its ability to push aside or lift heavy lumps of soil is notable. Its emergence above ground is said to take place usually during the night. When once above ground, growth takes place rapidly, from one to two inches daily until maturity is reached. Some "large" plants were reported as fully grown within a known period of ten days; also, one hundred and fifty plants were noted on a three-acre plot at one time (letter, Northrop).

While this fungus usually grows singly, there are instances of closely compacted sporophores up to nineteen in number, the bases being held firmly together by interlacing strands of mycelium and agglutinated soil (specimens, Clary). No reference has been found in any of the literature to this manner of growth.

The sporophore is differentiated into "foot," stipe and "head" even in very early stages of growth. The foot, invariably present, which suggested to Desvaux the generic name, consists of a solid mass of intermingled soil and hyphae which remains intact; slender, root-like processes—easily lost in collecting—issue from this irregularly enlarged base (PLATE 2, FIG. 1). The surrounding soil which has not been penetrated by hyphae is readily shaken off. We note that the larger the sporophore the larger the foot, and that what appears at times as a rather top-heavy plant is thereby provided with anchorage and balance in soil from which it might otherwise be displaced easily by heavy winds and seasonal, torrential rains. A study of soil habitat shows that *Podaxis* is primarily a sand plant, which, when finding conditions favorable elsewhere, *e.g.*, clay or adobe, continues to form hyphae and to accumulate soil. The fact that other species of fungi grown under different conditions acquire similar accumulations shows that this character is not peculiar to *Podaxis*.

The stipe inclusive of columella, up to twenty-six cm. in height (PLATE 6, FIG. 3), and up to one and one-half cm. in thickness—often described as "solid"—is found in young plants to be stuffed with a loose, floccose weft of parallel hyphae which extend to within three mm. of the lower end of the stipe (PLATE 3, FIGS. 3, 4). The columella continues to the summit of the peridium with which it is confluent by a narrow, fragile isthmus.

Attention is called to a variant form in which the columella fails to meet the peridium by one cm. (PLATE 5, A, FIG. 1). A single specimen of this type was collected in Indio, California (Smiley). Two other specimens are known, one in Patouillard's herbarium (Dodge), one in Cleland's, South Australia, no. *549* (**5**). It was Lloyd's opinion that such a plant might be entitled to generic rank; however, he made it a distinct species, calling it *Podaxon anomalus* (**25**, 992). It is identical with other plants in the same collection, except for the non-percurrent stipe. Inasmuch as these forms are so isolated and do not recur except as a rare variation, we are regarding them merely as "sports."

The stipe is frequently swollen in the region where it joins the margin of the peridium (PLATE 7, FIGS. 1, 3). Below the peridium the outer layers of the stipe are often lacerate horizontally, due to

the fact that they cannot keep pace with the more rapid growth taking place within (PLATE 5, A, FIGS. 1, 2).

A twist in the stipe (it may be left or right-handed), made the basis of a distinct species by Linnaeus, who was followed by subsequent botanists in this matter, is occasionally met (PLATE 3, a, b). A similar digression from the usual manner of growth has been observed in another sand plant of the Pacific Coast region—*Batarrea phalloides*[3] (Dicks.) Pers. The twist occasionally met in these two genera may not be considered sufficient ground to establish distinct species.

The peridium, up to 10 cm. in width, often presenting a mica-like gloss, is differentiated into two layers; the outer splits into thin, ligulate scales which often hang out loosely in active stages of growth, giving the plant a very shaggy appearance. The scales at the summit are quite firm in texture and are more permanent. Frequently sporophores are of a beautiful, snowy whiteness (Frontispiece, Palm Springs, Clary); it has been suggested that chemical examination of soils might throw some light on the extraordinary variations in the color of the exoperidium.

The scaly character of the peridium impressed the mind of Fries when he characterized Ehrenberg's plant as "peridio squamoso, stilidio demum denudato, stipite tenuiore" (**17**, 1829, p. 62). When the plant is fully mature, all the scales are shed, revealing a dingy, ochre-colored endoperidium (PLATE 5, B). In fact, scaliness and smoothness—made the occasion for marking off species by some authors—simply indicate different stages of development or maturity.

The endoperidium—three to four mm. thick—from the inner surface of which are produced the "tramal plates" (**1**, p. 318; **14**, p. 495) of the reproductive tissues, is firm and compact in texture.

The cylindric-elliptical chamber between the columella and the endoperidium is filled with a soft, pulpy glebal tissue which loosely spans the chamber. On "teasing out" these hymenial strands with a needle, they appear to be attached with equal firmness to the endoperidium and columella; in mature plants, however, these tissues are released first from the endoperidial wall and remain clinging to the columella, giving the appearance of a "bullrush" as suggested by Massee (**27**, 1890, p. 36), (see also PLATE 6, FIG. 5).

[3] Edwards, Colton, California.

The gleba in youngest plants is white; it gradually turns yellow, and often takes on some Indian red tones—described by Berkeley as that of the substance called "crocus"—which also appear as patches in the outer layers of the stipe and peridium (**2**, 1845; **4**, p. 291; PLATE 10).

There are only occasional evidences that deliquescence, noted in many Gasteromycetes, takes place here to a limited degree (PLATE 4, a, b).

MICROSCOPIC STUDY OF YOUNG PLANTS AND STUDY OF THE PHOTOMICROGRAPHS

The glebal elements are complex and superimposed to such an extent that it is difficult to make out their structure. Fructifying tissues consist of hyaline, rope-like strands which span the glebal chamber from the columella to the endoperidium; these strands branch repeatedly, thus creating a multitude of labyrinthine interspaces. The basidia, arranged in globoid clusters, issue from closely adjacent points of attachment on the tramal strands (PLATE 10, B). This is an arrangement such as is depicted by Fischer (**16**, 1900, p. 333) in his description of *Phellorinia Delestrei* with this exception: he figures basidia of uniform size, whereas, in our plant, they show great variation in size. The above is an important item because it indicates that basidia reach maturity successively, as noted in other species of Gasteromycetes (Lycoperdaceae), also of Hymenomycetes (**4**, II, pp. 266–455).

Each ovoid cell shown in plate 10, B, was interpreted by Massee as a monosporous ascus, so that he came to the conclusion that "*Podaxis* is an Ascomycete" (**27**, 1890, pp. 33, 69).

Examination of fresh young material received from the Indio garden made by Doctor Lee Bonar did not substantiate Massee's claim. Dr. Bonar was able to demonstrate beyond the shadow of a doubt that *Podaxis* has spores borne on basidia and is therefore a Basidiomycete. The wall of a ripe basidium, and particularly the attachment of spores to the basidium, are characterized by extreme delicacy of structure. Several basidia with four smooth, sessile, hyaline spores, not arranged in perfect regularity on the apices, were found *in situ* by Dr. Bonar and viewed by the writer. In one instance only two spores could be found. If the question is

asked, "What becomes of basidia after abscission has taken place?" here is de Bary's answer: "basidia, having given up their protoplasm to the formation of spores, are usually dissolved by processes of decomposition not accurately known" (**1**, pp. 68, 310), (**4**, II, pp. 312, 313).

We now proceed to a consideration of an application of the principle of "successive generations," a subject so fully elaborated by Buller (**4**, II, pp. 244–359) in his study of Hymenomycetes. Just how many of the fascicled cells (PLATE 10, B) might have become fertile had the plant remained in the ground and continued to grow no one can say. Conditions might be so favorable that a plant might ripen most of its basidia, or only a small number might come to maturity. Basing judgment on the mass of spores in a well developed plant, we incline to the first possibility.

No literature is found to assist in an interpretation of the reproductive tissues shown in plate 10. Buller discusses "past, present, coming and future 'generations' of basidia in Hymenomycetes" (**4**, I, p. 63);[4] there is undoubted evidence that a similar progressive ripening of spores takes place in this Gasteromycete. Very few spores are observed on a slide of very young material, more in older, and a limitless number in fully mature material. Our observations coincide with those of Fischer (**16**, 1900, p. 333), since he states that the sporophore of *Podaxis* matures from the base upward; also with those of Patouillard, who mentions that the ripening process takes place "graduellement" (**28**, 1890, p. 163). We may construe plate 10, B as indicating a "past generation" of collapsed basidia, because of the presence of ripe spores; no present generation as no spores are seen attached; also, "coming generations"—immature basidia which were arrested in their growth when the plant was collected. Basidia in the same field of view present marked variation in size.[5]

Inasmuch as several seconds or even minutes may elapse between the shedding of a set of spores from a given basidium

[4] He estimates that there are ten "generations" in *Panaeolus companulatus* (**4**, II, p. 267). See also his studies of *Stropharia semiglobata* and *Agaricus campestris* (**4**, II, pp. 327–455).

[5] A similar variation in size of basidia is figured by Maublanc and Malençon for *Battarraea Guicciardiniána* in Bull. Soc. Myc. Fr. **46**: *pl. 2* (1930), but not commented upon.

(Buller), it is possible to conceive—as ably demonstrated by Vokes (**45**) for a Hymenomycete—that spores may not necessarily be formed simultaneously in this Gasteromycete; of this there is indication but no proof. We may, therefore, postulate in *Podaxis* a perfected system of progressive ripening, existing not only in the glebal tissues throughout "from below upward," but also maintaining in the formation of spores in each individual basidium.

In the same plate is shown a large, highly vacuolated, ovoid cell—an abnormally large basidium, $45 \times 24\,\mu$.[6] A number of these appeared in a mount in 50 per cent lactic acid; such pronounced enlargement has not been observed in other preparations, and apparently represents an extreme variation.

We stated that the spores[7] in the material examined by us are sessile, the point of attachment making a scar (hilum); on it a fragment of the basidium may occasionally be seen hanging as a loose shred. Just opposite the point of attachment at the distal end there appears the single germ pore which appears hyaline by transmitted light, 2–2.5 μ diam., ending in a flattened circular disc (PLATE 10, A, B), (**1**, pp. 100, 101, 111).

The spores, with an average $10–13 \times 10–15\,\mu$, often present great variation in size (up to $36\,\mu$ long), also in shape (pear shaped, centrally constricted, irregular), not only in a single plant but even in a single mount (PLATE 10, A, B). Each spore is provided with a double integument which is colorless at first; the inner layer gradually takes on a garnet-brown tone (a yellowish-reddish brown) (**33**), and later a rich mahogany tone ("rouge acajon," **28**, 1890, p. 166). The yellow tone is derived from the protoplasmic content of the spore, which appears to hold granular material in suspension (**4**, I, p. 7; II, p. 304).

Spores *in situ* may be viewed only in young material, either fresh or preserved in fluid, and even then very rarely, in the ex-

[6] Considered "normal" by C. W. Dodge. See addendum.

[7] Dodge figures definite sterigmata on basidia in the American plant (**14**, 1931). Wakefield finds in our material "a slight neck which may be regarded as a suggestion of an abbreviated sterigma." [Patouillard figures short sterigmata for *P. arabicus* (**28**, 1887).] These extraordinary variations in the attachment of spores to basidia—from sessile to short neck—to definite sterigmata—observed in young material from a single collection from the Indio garden plot, furnish additional evidence to the single-species argument, considered in comments on published species.

perience of the writer. Lack of such material accounts for the taxonomic difficulties mentioned by de Bary (**1**, p. 317), and by Berkeley (**2**, 1857, p. 349).

It should be stated that whereas spores in Basidiomycetes may usually be seen to increase in size at the apices of basidia, we have seen only fairly good sized spores even in young material and no suggestion of sterigmata. Repeated efforts have been made to secure a germination of the spores of *Podaxis* in water, by subjecting them to temperatures ranging from 20° C. to 30° C., over varying periods of time, but without success.

CAPILLITIAL THREADS IN PODAXIS

These may be observed stretching irregularly in the trama of the glebal strands. They are free from the other glebal tissues, but are attached to the columella and to the endoperidium. They vary in diameter from 3.5 to 8 μ, average 5–6 μ (24 μ). They are abundant in material which is taken from near the central columella, less abundant if taken from near the endoperidium and frequently are altogether lacking elsewhere. In young plants the threads are hyaline, cylindrical, fairly straight, rarely septate or branched, and show not even the slightest indication of a spiral structure. In older plants the threads begin to take on garnet-brown tones, often become flattened and ribbon-like, and occasionally show distinct indications of a spiral within the wall. It seems necessary to emphasize these differences in the thread due simply to age, and marking different stages in its development, because they have been made the basis by different authors for segregating plants into species.

All that we have said descriptive of the thread in North American material applies to all foreign material except *Podaxon carcinomalis* Fries, from South Africa, in the Kew Herbarium (PLATE 12, A, B). This thread is thick-walled, somewhat rigid, deeply colored, varies in width from 6 to 19 μ, is occasionally branched and very much entangled. Only rarely does it separate along the lines of the striae, producing an open spiral. The same mounts used in the preliminary study were examined anew some months later, and the spirals then appeared to have straightened into "ribbons" (de Bary).

Berkeley (**2**, 1845) examined the Linnaean material of *Podaxis* and found nothing "unusual" in the thread of *L. pistillare* L., but he did find a spiral "here and there" in *L. carcinomale* (both in an excellent state of preservation in the Linnaean Society's rooms in London). We have found no thread in our twelve collections from South Africa comparable to that in the material received from Kew, which, accordingly, as far as our observations extend, is an unusual variation. This variation, however, is one of degree and not of kind. We have abundant evidence that *all* capillitial threads grow on spiral rather than on longitudinal lines, and are inclined to believe that we have here simply a more advanced state of maturity than has been met elsewhere.

Another type of thread—long, slender, straight, hyaline, like that in our American plants, was found in this very mature material (PLATE 12, A). The observations of the writer correspond with those of de Bary, who also found two aspects of the thread in one and the same plant—"*Podaxon pistillaris*,[8] some with rather thin, yellow walls, which flatten into ribbons, others with thick, yellowish-brown membranes which readily tear into spirals" (**1**, p. 318). The variation described simply represents different degrees of development.

The thread in the material, which came to us from South Brazil by courtesy of Professor Thaxter (PLATE 12, C), reveals a spiral thickening in the wall, and looks like a silken cord which, overtwisted, doubles back on itself rope-like (PLATE 12, C). This aspect of the thread is an exact counterpart of that observed in the South African material received from Wakefield.

We find, therefore, no reasonable ground for segregating into species the plants examined because of distinctions in the capillitial thread.

For function of thread see Massee (**27**, 1890, 1906), also Gynn-Vaughn, 1927. It is now generally conceded that *one* of the functions of the capillitial thread is to assist in the dissemination of spores.

[8] Herbarium at Berlin, marked Schweinfurth, no. *275*.

CITATION OF NORTH AMERICAN MATERIAL EXAMINED

Localities:

1. Bampo, Sonora, Mexico, type material of *Podaxon mexicanum* Ellis, Palmer, 1890. J. A. Stevenson.
2.* Phoenix, Arizona, McClatchie, 1898.
3. Calexico, Imperial Valley, Abrams, no. *3988*, 1903.
4.* Along the Colorado River, Palo Verde, Hall and Greata, April, 1905.
5.* Panamint Mountains, 5000 feet elevation, Hall and Chandler, May, 1906.
6. Sonora (Mexique), November, 1908, determined *P. Farlowii* by Patouillard, Musèum d'Histoire Naturelle, Paris. R. Heim.
7.* Imperial Valley, three collections, Bridwell, June, 1912.
8.* Colorado River, near Needles, Rixford, 1913.
9.* Yuma, Arizona, Hall, September, 1920.
10. Arizona, October, 1922, determined as *P. mexicanum* Ellis, by V. K. Charles. Smithsonian Institution, Washington, D. C.
11. Indio, California, Clark, June, 1926. From A. Eastwood.
12. Indio collection, J. L. Griffin, October 14, 1929.
13. Indio and Coachella Valley, approximately fifty specimens, Smileys, 1929–31.
14. El Centro, California, approximately three hundred specimens, Northrop, 1929–32.
15. Indio, Coachella Thermal and Palm Springs highways, also Mecca (40 miles east of Palm Springs area) over fifty specimens, Clarys, 1931.
16. Old Desert Road, Florence to Phoenix, Arizona; Casa Grande district, Phoenix, also Calexico, Edwards, 1929–31. Specimens reported, road from Mecca to Blythe, winter, 1932.
17. Casa Grande National Park, Coolidge, Arizona, C. P. Russell, March 1, 1932.
18. Santa Rosa Mountains, below Mt. Martinez; also, Coachella Valley, west of Narbonne Ranch, B. L. Clary, March 8, 1932.

* Herbarium, University of California.

19. Coral Reef Ranch, Coachella, California, B. Harwell, March 8, 1932.
20. East of Baker, near Mohave Desert, Mrs. G. E. Kelly, March 22, 1932.

CITATION OF FOREIGN MATERIAL EXAMINED

1. *Podaxon carcinomalis* Fries, "on ant hills," Uitenhage, Zeyher, no. *99,* det. Berkeley, Royal Botanic Gardens, Kew, England, E. M. Wakefield.
2. *P. "carcinomatis"* Fries, Cap-de-Bonne-Espérance, coll. de Drège, det. Léveille (puis Tulasne), no. *9454d,* Musèum d'Histoire Naturelle, Paris, R. Heim.
3. *P. "carcinomatis"* (L.) Fries, same locality and collector, det. Hariot (apr. Léveille et Tulsane), Musèum d'Histoire Naturelle, Paris, R. Heim.
4. *P. aegyptiacus* Mont., "Sahara occidental, Avril, 1923," Université d'Alger, R. Maire.
5. *P. aegyptiacus* Mont., "in arenosis, Avril, 1928, no. *1503,*" Université d'Alger, R. Maire.
6. *P. arabicus* Pat., "Sahara occidental, Avril, 1923," Université d'Alger, R. Maire.
7. *P. carcinomalis* Fries, "Garstfontein, Pretoria Dist., Transvaal, Apr., 1911." No. *1689,* Union South Africa, Dept. Agr., A. M. Bottomley.
8. *P. carcinomalis* Fries, Kroonstad, Orange Free State, December, 1930. No. *5585,* Union So. Africa, Dept. Agr., A. M. Bottomley.
9. *Podaxis carcinomalis* (L.) Desv. (one specimen in formalin and one dried). University of Cape Town, E. L. Stephens.
10. *Podaxon sp.* "from ant heap, Transvaal, So. Africa, March, 1926." University of the Witwatersrand, Johannesburg, E. M. Young.
11. *Podaxon sp.* "Ant heap, Johannesburg, June, 1927." University of the Witwatersrand, Johannesburg, E. M. Young.
12. *P. carcinomalis* L. var. *minor,* det. Lloyd, Pretoria, So. Africa, 27–2–21. J. A. Stevenson, Dept. Agriculture, Washington, D. C.

13.[9] *P. carcinomalis,* Univ. Stellenbosch, Union So. Africa. P. A. van der Bijl.

14. *P. carcinomalis,* " from S. Africa, MacOwen, Herb. Patouillard." Farlow Herbarium, Cambridge, Mass., R. Thaxter.

15. *P. carcinomalis* (L.) Fries, Is. of Maui, Hawaii, Shear and Stevens, Jan. 6, 1928.

16. *Podaxon* (?) " from termite nests in S. Brazil, von Höhnel, 1902." Farlow Herbarium, Cambridge, Mass., R. Thaxter.

17. *Podaxon* (?) " Kingston, Jamaica, Hitchcock no. 7, in *carcinomalis* cover." Farlow Herbarium, Cambridge, Mass., R. Thaxter.

18. *Podaxon squamosus* " from Patouillard's herbarium." The New York Botanical Garden, New York City.

19. *Podaxis pistillaris,* Cape Verde Is., det. Massee. The New York Botanical Garden, New York City.

TABULATION OF GENERA AND SPECIES WHICH HAVE BEEN PUBLISHED

1. *Lycoperdon pistillare* L.[10] Mant. Pl. 313. 1771.
2. *Scleroderma pistillare* Pers. Syst. Fung. 150. 1801.
3. *Schweinitzia pistillaris* Grev. Edin. Phil. Jour. **8**: 256–258, *pl. 6.* 1822–23.
4. *Cauloglossum pistillare* Grev. Scottish Crypt. Fl. **1**: 60. 1823.
5. *Podaxon pistillaris* Fries, Syst. Myc. **3**: 63 (described by Berk. Lond. Jour. Bot. **4**: 291–293. 1845). 1829.
6. *Lycoperdon carcinomale* L. Spec. Pl. Supp. ed. 13, C. L. fil. 453. 1781.
7. *Scleroderma carcinomale* Pers. Syst. Fung. 153. 1801.
8. *Schweinitzia carcinomalis* Grev. Edinb. Phil. Jour. **8**: 256–268. 1822–23.
9. *Cauloglossum carcinomale* Grev. Scottish Crypt. Fl. **1**: 60 1823.
10. *Podaxon carcinomalis* Fries, Syst. Myc. **3**: 62. 1829.

[9] " The only *Podaxon* known in the Union." Letter to Bonar, April 28, 1930.

[10] Linnaeus (1771) credits Boccone with a knowledge of this plant, refers to it as " fungus clavatus albicans, italicus pistillaris, sed colore differt." (See Musea di Fisica e di Esperienze, *plate 307,* 1668); also Koenig, who published in 1680, also Tournefort (1694) who quotes Boccone (**40**).

11. *Podaxon carcinomalis* var. *minor*, Jour. Bot. **28**: 75. 1890.
12. *Lycoperdon axatum* Bosc, Act. Soc. Hist. Nat. Paris **1**: 47, *pl. 11*. 1792.
13. *Podaxis axata*. Attributed to Bosc by Massee, Jour. Bot. **28**: 75. 1890. Also by Cooke. 1892.
14. *Podaxis senegalensis* Desv. Jour. de Bot. **2**: 97. 1809.
15. *Cionium senegalensis* Spreng. Syst. Veg. **4**: 529. 1827.
16. *Mitremyces indicus* Spreng. Syst. Veg. **4**: 518. 1827.
17. *Podaxon indicus* Spreng. Syst. Veg. **5**: 518. 1828. (**26**: p. 88.)
18. *Podaxon calyptratus* Fries, Syst. Myc. **3**: 62. 1829.
19. *Podaxon calyptratus* var. *minor* Cooke. 1879.
20. *Podaxon aegyptiacus* Mont. Ann. Sci. Nat. II. **20**: 69. 1843
21. *Cauloglossum aegyptiacum* Zobel in Corda, Ic. Fung. **6**: 18. 1854. (Zobel lists *P. aegyptiacum* Mont. as a synonym.)
22. *Podaxon loandensis* Welw. & Currey, Trans. Linn. Soc. Lond. **26**: 279–94, *pls. 19, 20*. 1850–1861.
23. *Podaxon elatus* Welw. & Currey, Trans. Linn. Soc. Lond. **26**: 288, *pl. 19, f. 4–6*. 1850.
24. *Podaxon mossamadensis* Welw. & Currey, Trans. Linn. Soc. Lond. **26**: 288, *pl. 19*. 1850.
25. *Podaxon mossamadensis* var. *Emini* Henn. Fung. Afr. II, p. 38 (See Sacc. Syll. Fung. **11**: 158). 1893.
26. *Podaxon Warnei* Peck, Bull. Torrey Club **9**: 2. 1882.
27. *Podaxon Emerici* Berk. (as per Mass.) Jour. Bot. **28**: 77. 1890.
28. *Podaxon arabicus* Pat. Bull. Soc. Myc. Fr. **3**: 122, 123, *pl. 11, f. 1, 2*, a; *ibid.*, **6**: 166, 167, *pl. 17, f. 3*. 1887.
29. *Podaxon Deflersii* Pat. Bull. Soc. Myc. Fr. **6**: 165, *pl. 17, f. 1*. 1890.
30. *Podaxon Schweinfurthii* Pat. Bull. Soc. Myc. Fr. **6**: 165, *pl. 17, f. 2*. 1890.
31. *Podaxon squamosus* Pat. Bull. Soc. Myc. Fr. **7**: 210, *pl. 13*. 1891.
32. *Podaxon Perraldieri* Pat. Cat. Pl. Ceil. Tunisie 68. 1897.
33. *Podaxon Chevalieri* Pat. & Har. Champ. Senegal, Jour. Bot. **14**: 241, *pl. 7*. 1900.
34. *Podaxon algericus* Pat. Bull. Soc. Myc. Fr. **20**: 53, *pl. 5*. 1904.

35. *Podaxon Glaziovii* Henn. Hedwigia **36**: 210. 1897.
36. *Podaxon ghattasensis* Henn. Hedwigia **37**: 287. 1898.
37. *Podaxon Gollani* Henn. Hedwigia **40**: 338. 1901.
38. *Podaxon Mülleri* Henn. Hedwigia **43**: 187. 1904.
39. *Podaxon mexicanum*[11] Ellis, Jour. Myc. **7**: 274. 1893.
40. *Podaxon argentinus* Speg. Anal. Mus. Nac. Buenos Aires **6**: 186. 1899.
41. *Podaxon patagonicus* Speg. Anal. Mus. Nac. Buenos Aires **6**: 186. 1899.
42. *Podaxon macrosporus* Speg. Anal. Mus. Nac. Buenos Aires **16**: 27, *cum icon.* 1906.
43. *Podaxon strobilaceus* Copeland, Ann. Myc. **2**: 4, *pl. 1, f. 7.* 1904.
44. *Podaxon termitophilus* Jumelle & Perrier, Compt. Rend. Acad. Paris **145**: 274; Sacc. **21**: 469. 1907.
45. *Podaxon anomalus* Lloyd, Myc. Writ. **6**: 992. 1920.
46. *Podaxon* sp. Jamaica. Farlow Herb. (Hitchcock). 1891.
47. *Podaxon* sp. So. Brazil. Farlow Herb. (von Höhnel Herb.).
48. *Podaxon Ferrandi* Mott. Somalie, Africa. Patouillard's Herb. (Thaxter).
49. *Podaxon Paoli* Berk. (?) Canary Is.
50. *Podaxis Farlowii* Massee, Jour. Bot. **28**: 77. 1890.
51. *Podaxon Farlowii* form *gracilis* Pat. Mexico. 1908.
52. *Podaxis pistillaris* (L.) Fries, Comp. Morph. Fungi, Gäumann-Dodge. 1928.

COMMENTS ON THE ABOVE

1, 6. *Lycoperdon pistillare* L. (1771). From East India. The first description of the plant reads: "clavatum, stipite torto, fungus spithameus, croceus. Stipes bafi ovata, cylindricus, totus fibris longitudinalibus tortus. Clava terminalis ovato-oblonga, stipite quadruplo craffior, duplo longior, veftitus membrana crocea, repleta pulvere ferrugineo. India, *Koenig.*" The species *L. carcinomale*, published ten years later (1781), is described as clubbed, stipe cylindrical, straight (cancerous); Cape of Good Hope, *Thunberg;* both, dusty, rooted, replete with farinaceous seeds.

[11] Error in ending of specific name.

Miss E. M. Wakefield describes the Linnaean material as follows: "*L. pistillare* is a small plant, with a slender, twisted stem, which suddenly expands into a sandy, bulbous base. The peridium occupies a relatively small proportion of the stem, and is distinctly dark, red-brown in color. It is a peculiar color, not at all rusty. In *L. carcinomale* the stem is stouter, and is more gradually thickened downward. The peridium occupies about half the height of the stem and is umber-brown, with no hint of red. Microscopic examination was not allowed." (Letter, October 9, 1931.) For Berkeley's examination of capillitial threads in the Linnaean material see page 10.

Specimens of the American plant with straight and twisted stipes may be found growing side by side. Probably the Linnaean plants are one species, *P. carcinomalis,* a little more mature (See Berk.'s detailed description of *P. pistillaris,* 1845).

2, 7. Persoon (1801) retained Linnaeus' two species, but placed them in another genus, *Scleroderma.* Providing Persoon's material were without scales, very mature and well-weathered like our Phoenix, Arizona, specimens, it might readily have suggested to him that genus.

11. *Podaxon carcinomalis* var. *minor* is ascribed to Berkeley by Massee. This name was not published by Berkeley,[12] neither does it appear in the manuscript index to his herbarium.

12. *Lycoperdon axatum* Bosc (1792) = *P. calyptratus* Fries, from an island in the Sénégal River, West Africa (**39**, p. 362). Following is Bosc's description:

"*Lycoperdon stipitatum*, clavatum, stipite torto lignoso ad apicem clavae praelongo, clava lateribus lacérato-déhiscente.

Habitat ad Sénégalem fluvium.

Racine tubéreuse, oblonguè, terminée par un prolongement.

Tige fistuleuse, d'une substance presque ligneuse dont les fibres se contournent de gauche à droité. Cette tige se prolonge jusqu'au sommet de la tête.

Tête ovale, de quatre pouces de long sur deux de large,

[12] Letter, E. M. Wakefield, May 6, 1930.

entourant la partie supérieure de la tige. La membrane extérieure se fendant, au moment de la maturité, dans plusieurs endroits des parties latérales inférieures, pour laisser échapper les semences. On remarque au sommet de cette tête deux ou trois membranes ovoïdes, irrégulières, qui ne sont attachées que par un point, mais qui restent appliquées à la surface. Elles sont les restes du volva.

Semences de même nature et de même couleur que dans le L. bovista. Elles sont arrêtées dans un réseau fixé à l'axe de la tête. Ce réseau ne paroît attaché en aucune manière à la membrane extérieure.

Le *Lycoperdon axatum* a environ un pied de haut d'une de ses extrémités à l'autre. Sa couleur est d'un gris blanchâtre semblable à celle du *Lycoperdon pedunculatum.* Il paroît avoir des rapports avec le *Lycoperdon pistillare* et le *Lycoperdon carcinomale.* Il présente des caractères qui n'ont pas encore été observés dans les champignons, tels que le prolongement de la tige jusqu'au sommet de la tête, et le déchirement latéral de cette meme tête pour la dispersion des semences. Il semble faire le passage entre les *Lycoperdon,* les *Clathrus* et les *Clavaria.*

Cette belle espèce a été trouvée par M. Roussillon dans une petite île sablonneuse du fleuve Sénégal, peu éuloignée du comptoir français. Elle fait partie des richesses botaniques et zoologiques que ce zélé naturaliste a rapportées d'Afrique.

La figure de la Planche VI représente ce champignon de grandeur naturelle, mais par erreur du graveur, les fibres sont contournées en sens contraire de ce qu'elles doivent être.

On observe que la racine ne paroît si grosse, que parce qu'elle est entourée d'un sable fortement aglutiné, au moyen d'une liqueur visqueuse."

Bosc wished to emphasize the character of the stipe elongated as an axis into the peridium. All characters listed in his detailed description are identical with those of an American plant with twisted stipe. Probably a justifiable reduction here. He interpreted the scales closely adherent at summit of peridium as remnants of a volva!

13. *Podaxis axata,* from New South Wales, based on scanty capillitium, is ascribed to Bosc and so published by Massee and Patouillard (1890), also by Cooke (1892). We do not find that Bosc ever used this combination; possibly it is

an unpublished name of Bosc which may be quoted as *P. axata* Bosc (*fide* Massee, Patouillard and Cooke).

3, 4, 8, 9. Greville (1822) was not satisfied with either of the generic names *Lycoperdon* or *Scleroderma;* he states that if Persoon had dissected his plant, he could not have placed it in *Scleroderma.* Accordingly he proposed the genus *Schweinitzia,* retaining Linnaeus' and Persoon's two species. He had his misgivings, however, as to the validity of *S. carcinomalis* (from Cape of Good Hope, in mounds of termites), asking, "an species distincta?" (**18**, 1822, p. 258). Like Bosc he emphasized percurrent stipe and mode of dehiscence. Finding his generic name preoccupied by Elliot's genus of phanerogams, he changed the name to *Cauloglossum* in 1823, apparently in ignorance of Desvaux' name (**18**).

14. Desvaux (1809) based his *Podaxis senegalensis,* from the banks of Sénégal River, on Bosc's plant. He gives a detailed description, stipe twisted from left to right, peridium double, mentions attachment of columella to peridium, also deals with relationships and taxonomic position. It appears that Desvaux was not justified in ignoring the various specific names which had been proposed by other authors. The description indicates such a full correspondence with the American plant that we feel justified in specific reduction. The new generic name is descriptive and satisfactory.

15. Sprengel placed Desvaux' plant in *Cionium* as *C. senegalensis* (Desv.) Spreng. It is stated by Fries (**17**, p. 63), also by Streinz (**39**, p. 454) to be equivalent to *P. calyptratus,* which our plant blankets. Though we have not been able to refer to Sprengel's text, reduction seems to be justified.

16, 17. *Mitremyces indicus* Spreng., later called by him *Podaxon indicus* (**26**, p. 88) = *P. pistillaris* (**39**, p. 455) has been described by numerous authors; their descriptions tally so perfectly with some of our plants that it appears reasonable to reduce it.

5, 10, 18. Fries (1829) renamed Bosc's plant as *P. calyptratus,* also cited the figure "ad Senegal fluvium (*v. ic.*)," implying that he had not seen a specimen; he ascribed the

twisted stipe character of *P. pistillaris* also to this species, adding for characterization a removable peridium and exceptionally massive base; He made *P. carcinomalis* inclusive of tall, straight-stemmed plants, and *P. pistillaris* of shorter, stocky plants.

19. *Podaxon calyptratus* var. *minor* Cooke. Very small plants with peridia, which in the ripe state can be lifted off intact, occur very frequently in our material.
20. *P. aegyptiacus*[13] Mont. Two specimens determined by Dr. Maire and sent to us have the same irregularity in size and shape of spores as our small plants from Indio, California.
21. *Cauloglossum aegyptiacum* Zobel. Zobel published this species twelve years after Corda's death, stating that he received his material from Montagne. He described and figured the plant as having a volva, a single-layered peridium with dehiscence at the sides. This plant must belong in some other genus not *Cauloglossum* Grev.
22. *Podaxon loandensis* Welw. & Currey, no. *115,* suggests our tall slender plants with twisted stipes. "Paulo post primas pluvias adparet."
23. *Podaxon elatus* Welw. & Currey, no. *148,* 31 cm. tall (Saccardo) must have been the most massive of the West African plants collected by Welwitch and Currey. They record capillitium sometimes spirally ruptured.
24. *Podaxon mossamadensis* Welw. & Currey, no. *149,* is described as a smaller plant. Every character mentioned in the descriptions of their three species is found in the American plant; also verified by good figures. The authors mention absence of spiral markings in the thread, and state that these vary according to age of the plant. Spores 10 μ diam.
25. *Podaxon mossamadensis* var. *Emini* Henn. From Central Africa. No check. Spores 8–12 $\times$ 6–8 μ.
26. *Podaxon Warnei* Peck. Later referred by Peck to *Secotium Warnei* (**29**, 1882), really belongs in *Endoptychum,* not closely related to *Secotium.* In wrong genus (letter, Dodge).

[13] L. E. Melchers records seven species of *Podaxis* in Egypt. See Trans. Kansas Acad. Sci. **34**: 61, 1931.

27. *Podaxon Emerici* Berk. Described by Massee as containing both basidiomycetous and ascomycetous fructification. We are unable to check this point in *P. Emerici,* but Massee's claim is not supported by the findings of more recent workers. We find the fascicled arrangement of basidia in the American plant perplexing and one which we can understand might have been interpreted by Massee as consisting of monosporous asci. In fact, C. W. Dodge calls attention to a fascicled arrangement of asci frequently met in many groups of Ascomycetes, *e.g., Mesophellia.*[14] That there are basidia in *Podaxis*—confirmed by several mycologists—may be definitely alleged; that there is also ascomycetous fructification as published by Massee has never been demonstrated.

    Patouillard classified fifteen[15] species and two forms (seven "new," three from America), according to color or absence of color in the basidia ("basides"). This procedure has been found to be ill-advised, because color in the fructifying parts is entirely dependent on the age of the plant. No item appears in any of his descriptions, including spore measurements, which is not covered by our American material.

28. *Podaxon arabicus* Pat. Canal in columella was noted, capillitium colorless, scanty, spores subglobose or ovoid, spores 11–12 × 8–9 μ.

29. *Podaxon Deflersii* Pat. "Capillitium nul." Patouillard notes short sterigmata. Spores 10–12 × 6–9 μ.

30. *Podaxon Schweinfurthii* Pat. "Ecailles appliquéed." Gleba yellow, later orange-red. Small hilum visible. Spores 11–16 × 8–10 μ.

31. *Podaxon squamosus* Pat. From Egypt, Arabia, Syria. Stipe longitudinally striate, a slender plant, close to *P. carcinomalis,* capillitium a spiral ribbon, colorless. Basidium four-spored; spores subsessile, truncate at apex, with single pore. Spores 10–12 × 8–9 μ.

[14] Letter. March 9, 1932.

[15] Lloyd remarked facetiously that there appeared to be as many species of *Podaxis* as collections!

32. *Podaxon Perraldieri* Pat. "Columella percursa." "Capillitium non spiraliter." "*P. indico* Fries affinis." "In sabulosis (gravel) in Tunisia." Spores 14–15 × 10–12 μ.
33. *Podaxon Chevalieri* Pat. & Har. "Capillitio non spiraliter." From "Tombouctou," West Africa. Characterized as "eximia species" by Saccardo. Spores 12–13 × 8–10 μ.
34. *Podaxon algericus* Pat. Based on small sized plants and on changing colors in the gleba. His figure shows a perfectly white gleba (plant young) except in the region where peridium meets the stipe (change in color starts there). Basidia 2–4 spored. Spores 10–12 × 9–10 μ.
35. *Podaxon Glaziovii* Henn. From Brazil. No characters named in the text distinct from those of the North American plants. Spores 9–12 × 8–10 μ.
36. *Podaxon ghattasensis* Henn. From Central Africa. Resembles *P. elatus* Welw. & Currey. No distinguishing characters listed. Spores 12–14 × 7½–8½ μ.
37. *Podaxon Gollani* Henn. A very small slender plant from the Sahara Desert. Spores 10–12 × 8–10 μ. There is a possibility that the specimen determined by Lloyd as *P. carcinomalis* var. *minor,* from Africa may be identical.
38. *Podaxon Mülleri* Henn. From Goscogne River, Australia. No distinguishing character. Spores 10–16 × 10–12 μ.
39. *Podaxon mexicanum* Ellis. Gleba from his type specimen shows exact correspondence with our plant; also, his detailed description fits perfectly. In describing this "new" species, Ellis appears to have ignored the work of his predecessors and contemporaries. Spores 8–12 μ diam. (12–15).
40. *Podaxon argentinus* Speg. Spores very small, 4–5 μ diam. No check on this plant. We might expect another species here.
41. *Podaxon patagonicus* Speg. Very low in stature, spores slightly larger than those in no. 40, 5–6 μ diam. He suggests that this might be a "variety" of the above. (Our specimens from northern latitudinal range are also small, but show no microscopical differentiation.)
42. *Podaxon macrosporus* Speg. Spores larger, 14–18 × 7–12 μ,

blanketed by our plant. Habitat, arid stony hills called Zonda, "prope San Juan Argentinae." Sacc. Syll. Fung. **21**: 468, 469. 1912.

44. *Podaxon termitophilus* Jumelle & Perrier. From Madagascar, occurring in nests of termites.[16] "Basi inflato," related to *P. carcinomalis* and *P. squamosus*, differing from them chiefly in the color of the spores (Sacc.).

Plants described and figured by Verwoerd (**44**), showing several specimens toward the summit of an immense termite mound, could readily be mistaken in general appearance for American plants. Spores $12 \times 9\ \mu$.

45. *Podaxon anomalus* Lloyd (**25**, 1920, fig. 1776). To be regarded as a "sport" and not as a distinct species. "No true capillitium." "Spores $10–12 \times 12–14\ \mu$" (Lloyd). See description, p. 4, also PLATE 5, A1.

46. *Podaxon* sp. From Jamaica. We have examined gleba and it shows no character which distinguishes it from other North American material examined. It is of interest because it represents a transitional locality between the two western continents.

47.[17] *Podaxon* sp. from South Brazil.

48.[17] *P. Ferrandi* Mott, from Abyssinia.

49.[17] *P. Paoli* Berk. (?) Canary Islands.

50. *Podaxis Farlowii* Massee. Massee classified seven species according to a scarcity or abundance of capillitium. The amount of capillitium depends on the age of the plant and on the place in the glebal chamber from which material is taken, as previously explained.

The "new" species erected for the American plant is characterized by him as having "peridium broadest at the apex, stem slightly or not at all swollen at the base, capil-

[16] That there is any association between *Podaxis* and termites—Massee mentions "fungus-gardens" in this connection—seems improbable; a habitat of this kind has been rarely mentioned.

The fungus is said to be eaten by natives in Africa and Afghanistan, also said to be applied by them to cure cancerous sores (Linn.), *carcinoma* = cancer; called "Kraaisnuif"—crows' snuff—in South Africa (letter, Stephens).

[17] These are known to us only by name.

litium threads very rare, spores 10–12 or $10 \times 12\,\mu$, Arizona, Palmer" (**27**, p. 76). This characterization is inadequate and the claim for a "new" species is not supported by comparative studies. There is a possibility that the spores in our plants may average slightly broader and have greater brilliancy than those in our foreign material; however, the writer does not find such variations a sufficient basis for segregating into species, as previously stated.

Harkness (1880) published two species from the Colorado Desert. Lloyd reiterated that we have one species only—*P. Farlowii;* a collection in the Farlow Herbarium, originally named *Podaxon carcinomalis* by Farlow was later changed to read: *P. Farlowii.*[18]

51. *P. Farlowii* form *gracilis*[19] Pat., from Mexico.

52. *Podaxis pistillaris* (L. ex Pers.) Fries. Comprehensive of *all* the plants studied. This combination, which we believe is correct, has already been used by Gäumann-Dodge (1928). For adoption of *Podaxis* as a generic name see a subsequent topic. Fries' orthographic correction is allowed, see Rule 24, last clause, Art. 57.[20] Persoon's name is introduced because his Synopsis, 1801, is the starting point of nomenclature. See Rule.

EXCLUDED:

21. *Cauloglossum aegyptiacum* (Mont.) Zobel probably should be referred to some other genus. Zobel added for characterization of genus—"fungi volvati vel velati"—not proposed by either Greville, author of the genus, or by Corda or Fries when they published it. See page 19.

26. *Podaxon Warnei* Peck belongs in *Endoptychum* Czern. See footnote, p. 25.

43. *Podaxon strobilaceus* Copeland seems to be *Gyrophragmium Delilei* Mont. (= *G. decipiens* Peck).

Notes: 1. This fungus has been described under eight generic names: *Cauloglossum, Cionium, Lycoperdon, Mitremyces,*

[18] Letter, Thaxter, April 24, 1930.

[19] Known to us only by name.

[20] Règles Internationales de la nomenclature rédigées par John Briquet, Jena: Gustav Fischer, 1912.

Podaxis, Podaxon, Schweinitzia, Scleroderma. 2. Saccardo records the descriptions of twenty-five species inclusive of one variety.

PREFERENCE FOR PODAXIS AS A GENERIC NAME

Of the two generic names, *Podaxis* Desv. (1809) and *Podaxon* Fries (1829), the latter, it must be admitted, is in more common use. It has been aptly said that a scientific name is really only a symbol. We use Desvaux' cleverly devised name because of its priority claim of twenty years, and are not alone in so doing (Dodge, Massee, Cooke). It was Fries' notion that a name might not be derived from two languages (in this case Greek and Latin), and he accordingly states that "nomen *Podaxon* scribendum est" (**17**, 1829, p. 62). This opinion is not supported by the practice of recent botanists and mycologists in all cases. Inasmuch as it is generally conceded that priority is the underlying principle of all botanical nomenclature, that Gasteromycetes are usually referred to the authors who preceded Fries, and as many hybrid [21] words have found their way into standard dictionaries, *Podaxis* is retained as a generic name.

AFFINITIES

Phellorinia [22] Berk. "gen. nov." (Lond. Jour. Bot. **2**: 421) is the nearest known relative of *Podaxis*.

Members of this genus are distinguished from those of *Podaxis* chiefly because stipes are not percurrent. The arrangement of fascicled basidia in both genera, as described and figured by Fischer (**16**, 1900), suggests the hymenium of *Alpova* (**14**). See also Cooke for *Xylopodium* (**9**, 1892, p. 242, *pl. 16, f. 123*).

It has been stated by several authors, Hollós, Fischer, Peck, Saccardo, Lloyd, Coker and Couch, that *Phellorinia* occurs in southwest United States. Peck describes *P. californica* sp. nov. from two small specimens collected by S. B. and W. F. Parish in the Mohave Desert (north of Colorado Desert), 1882, "shaped like a broad wine glass" (**29**, 1890).

We have from H. E. Roberts one specimen of *P. macrospora*

[21] E.g. *Pseudotsuga, Hesperoyucca*, anglophobia, automotive, aeroplane.
[22] Incl. *Xylopodium* Mont. (**16**, 1900, p. 334). See also Grevillea **15**: 95.

Lloyd, collected from the Mohave Desert, near Needles, April 17, 1931 (see Lloyd, **25**, 1913, Letter 44, note 50).

Lloyd states that *P. inquinans* Berk. has been collected in Australia, Tunis, Texas, California. He claims that there are only two species of *Phellorinia, P. Delestrei* Dur. & Mont. and *P. strobilina* Kalch.—"among the rarest of Gasteromycetes." We have received from our foreign correspondents (Cleland, Australia; Stephens and Bottomley, So. Africa) specimens which appear to represent two distinct species, which with our own from the Mohave Desert make three in our collections. Fischer states that there are nine species of *Phellorinia;* Saccardo records four.

Chainoderma Massee. *C. Drummondii* is described by Cooke (**9**, 1890, **19**: 46; 1892, p. 221) as occurring near the Swan River, Australia; a small plant, 5–6 cm. tall by 1.5 cm. wide, stipe percurrent, peridium never released from the stipe, "remains of sterigmata usually persistent." Our depauperate, undeveloped forms of *Podaxis* from the Colorado Desert (PLATE 3, c) fit their descriptions in every particular. Such forms appear to be the result of excessive heat and diminished moisture supply. These stunted, dwarfed plants suggest the possibility that *Chainoderma* is not a valid genus. No reference appears to have been made to the genus either by Cleland or Lloyd in listing Australian fungi. It is described by Fischer.

TAXONOMIC POSITION OF PODAXIS

Nothing conclusive may be said concerning the taxonomic position in a phylogenetic scheme. *Podaxis* appears to be an aberrant genus, represented by a single species, possessing characters of several groups. It may have arisen, via *Leucogaster* and *Alpova* from the Ascomycetes—from a white-spored group of Plectoforms which are distinguished by unorganized hymenia (spores of young *Podaxis* are colorless).

Because of its axial, sterile columella, *Podaxis* suggests both *Secotium* [23] and *Endoptychum,*[23] but is closer to the latter because

[23] It is the opinion of C. W. Dodge, who has studied the type forms, that the Conard *Secotium agaricoides* is *Endoptychum* Czern. The latter genus has a powdery gleba, while Cunningham's *S. erythrocephalum* and *S. novaezealandiae* (**12**) have been shown by him to have gelatinous glebae which delequesce into slime; these species are only remotely related in their development to *E. agaricoides.* Dodge states: "*S. tenuipes* Setch. is a true *Secotium* of your flora." Letter, May 26, 1931.

of its powdery gleba at maturity. It shows resemblance to Lycoperdaceae, particularly to the stalked puffballs, *Phellorinia, Batarraea,*[24] *Tulostoma,*[24] *Calostoma* Desv. (= *Mitremyces* Nees), and seemingly ends with Lycoperdaceae.

It has been the practice of taxonomists, e.g., Saccardo, Clements, Dodge, Lloyd, to associate *Podaxis, Secotium, Gyrophragmium* in a group, naming it Secotieae or Podaxineae. The origin of *Secotium agaricoides* as described by Conard (**8**) is related to that of *Agaricus campestris* and *A. Rodmani;* he regards *Secotium agaricoides* as "a primitive or arrested agaric"—perhaps a paedogenetic form which comes to maturity in the "button" stage. To quote from Conard, "*Secotium* is a morphological intermediate between the Agarics and Gasteromycetes" (**8**, 1912, p. 108). It has been demonstrated in this laboratory that the early stages of *Podaxis* have absolutely nothing in common with those of Conrad's *Secotium.* Twenty-five years earlier even, de Bary wrote: "It is plain that *Secotium* (*i.e. S. agaricoides*) arranged in one special group along with *Podaxon* is founded only on superficial resemblance and is not tenable, and that such arrangement must be broken up" (**1**, p. 319). It thus appears that *Podaxis* does not even approach *Secotium* of Conard (*Endoptychum*) or Cunningham at any point in its life history.

While no histological studies of *Gyrophragmium* have ever been made, it is the opinion of the writer that this genus along with *Endoptychum* will be found to constitute a transition between the two large groups, Gasteromycetes (Lycoperdales) and Hymenomycetes.

Podaxis, notwithstanding its strong external resemblance to *Coprinus comatus,* especially in the young stages, is out of place in the table presented by Underwood who shows *Podaxis* removed from *Agaricus* only by the two genera, *Coprinus* and *Montagnites* (**43**).

Phellorinia Berk. is the only well known affinity. The validity of *Chainoderma* Mass. is questioned. *Cauloglossum* Grev. does not enter into the discussion since it is a synonym of *Podaxis* based on the same *Podaxis pistillaris* and *P. carcinomalis. Rhacophyllus* Berk. may be found to bear a relationship to *Podaxis.*

[24] Spelling of the author Persoon.

In view of findings to date, *Podaxis,* together with any other plants [25] which shall be found to have a corresponding arrangement of fascicled basidia, also powdery glebae at maturity may constitute a tribe of Lycoperdaceae to be called Podaxineae.

SUMMARY

Podaxis is found within the fortieth parallels north and south of the equator approximately. Its altitudinal range extends from sixty-five feet below sea level to five thousand feet above. An examination of a large amount of material collected from the southwestern regions of the United States shows great macroscopic and microscopic variations. Spores vary notably in size and shape. The capillitial thread is spiral in structure; spiralinity may be observed occasionally in fairly mature material. Only one North American species of *Podaxis* is known.

An examination of Old World material shows precisely the same types of variation. Basidia, spores and capillitial threads in both Old and New World material show similar, progressive stages of development, conditioned by the age of the plant. Every specimen examined is therefore referable to one species, *Podaxis pistillaris* (L. ex Pers.) Fries. Species reduced to *P. pistillaris* are: *Lycoperdon carcinomale* L., *L. axatum* Bosc, *Podaxis senegalensis* Desv., *Mitremyces indicus* Spreng, *Podaxon calyptratus* Fries, *Podaxon loandensis* Welw. & Currey, *P. elatus* Welw. & Currey, *P. mossamadensis* Welw. & Currey, *P. Emerici* Berk., *Podaxis Farlowii* Mass., *Podaxon mexicanum* Ellis, *P. arabicus* Pat., *P. Deflersii* Pat., *P. Schweinfurthii* Pat., *P. squamosus* Pat., *P. Perraldieri* Pat., *P. Chevalieri* Pat., *P. algericus* Pat., *P. Glaziovii* Henn., *P. ghattasensis* Henn., *P. Gollani* Henn., *P. Mülleri, P. macrosporus* Speg., *P. termitophilus* Jumelle & Perrier, *P. anomolus* Lloyd.

Species probably to be reduced are: *Podaxon argentinus* Speg., *P. patagonicus* Speg., *P. Paoli* Berk. (?) (Canary Is.), *P. Ferrandi* Mott (Abyssinia).

The fascicled arrangement of basidia found in *Podaxis* and

[25] "I think it is quite likely that eventually we shall find a group with a more or less independent evolution, having this common mode of spore production" (fascicled basidia). Letter, C. W. Dodge, May 26, 1931. See also his *Alpova* paper (**14**, 1931).

Phellorinia, in place of a palisade or even irregular arrangement (Sclerodermataceae), is most unusual in Basidiomycetes. Such unorganized hymenia suggest a possible relationship with certain Ascomycetes, *e.g., Leucogaster, Alpova* (**14**) (**47**). *Podaxis* and *Phellorinia* seem to constitute a tribe of the family Lycoperdaceae. An association with *Secotium* as described by either Conard or Cunningham is not justified because of a lack of correspondence in their glebal tissues.

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The writer wishes to make grateful acknowledgment to Professor Lee Bonar and Doctor E. B. Copeland, Department of Botany, University of California, also to other members of this faculty who have given helpful suggestions from time to time; to the late Professor Roland Thaxter, Farlow Herbarium, Harvard University; to Professor C. W. Dodge, Washington University, and Mycologist, Missouri Botanical Garden, who has critically reviewed this paper as well as studied some of the material; to Doctor C. L. Shear and John A. Stevenson, United States Department of Agriculture, Washington, D. C.; to Miss E. M. Wakefield, Mycologist, Royal Botanic Gardens, Kew, England; also to Dr. Fred J. Seaver, The New York Botanical Garden; and to many other officials, and particularly to the numerous collectors who have made this work possible.

These studies have been made in the hope that interest in a long-observed and variously named group of plants may revive; that reports from localities not yet heard from may come in; that further data especially concerning relationships of *Podaxis* may be supplied.

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EXPLANATION OF PLATES

Photographs and Photomicrographs by W. C. Matthews

PLATES 2–5 (FIGS. 1–7)

"SEVEN AGES" OF PODAXIS

Figs. 1, 1. Very young plants, root processes in place early differentiated into "foot" and head.

Fig. 2. Older, foot well developed, outer tissues split into ligulate scales.

Fig. 3. Still older, gleba (at first white) takes on a pale yellow-mahogany tone. Stipe, continuous through the peridium with narrow attachment at the summit, shows a central canal filled with a longitudinal weft of floccose hyphae.

Fig. 4. Vertical section of an older plant with gleba more deeply colored. Columella—the elongated stipe—has become detached from the endoperidium. Indio, California (Smiley). *a, b,* pl. 3: Left and right-handed twists in the stipe. *c:* An unsymmetrical, "depauperate" plant, never reaching maturity (frequently met).

Fig. 5, pl. 2. Much older plant with "perfect foot," peridium broadest at the summit (rare) shows no indication of release from the stipe. Scales have taken on a mica-like gloss.

Fig. 6, pl. 4. Gleba entirely ripe, peridium ready to be shed, calyptra-like. Note hoof-shaped foot. Head was held down by a heavy clod of adobe. *a, b:* A limited delequescence appears in the walls of peridia and as a drip down the stipe. El Centro, California (Northrop). See also, pl. 2, *a.*

Fig. 7, pl. 5, *B.* Endoperidium entirely denuded of scales, well weathered and polished. From clay river bottom, Casa Grande Valley, Phoenix, Arizona (Edwards). Plants may have remained *in situ* for an indefinite period of time. The two small plants, from Battle Creek Meadows, northern latitudinal range—40°—California (Jepson).

Plate 5, *A,* 1, 1. *Podaxis pistillaris,* a "sport," in which the thick fibrous columella fails to reach the endoperidium by one cm. (see, also, plate 9; extremely rare). Otherwise, no distinction in structure. Scales in actively

growing plant often hang out loosely. 2: Columella attached by a narrow isthmus, gleba pale orange-yellow, outer tissues of stipe split horizontally. Indio, California (Smiley).

PLATE 6

Figs. 1, 2, 3, show great variation in stature and in proportions of peridia; fig. 3, the tallest of all American plants collected, 26 cm. (Northrop).

Figs. 4, 5, show stipes longer than heads; fig. 5, the "bullrush" (Massee), gleba intact, was more firmly attached to columella than to endoperidium. Fig. 2, of snowy whiteness, retains its whiteness when dried, from Palm Springs, California. See, also, plate 1, frontispiece (Clary). Note variations in thickness of stipes.

PLATES 7 AND 8

Figs. 1, 2, 3. Robust plants, "fungus spithameus" (a hand span) (Fries), stipes short in comparison with peridia. Peridium at first tightly closed (1), later loosened at margin and splits from below upward (2, 3). Stipe enlarged in region of juncture with peridial margin (1, 3).

Fig. 4. Cespitose, clusters up to nineteen in number, have been noted (Smiley, Clary). Scales becoming dingy are gradually dried and worn away by wind or rain. Foot often pronged (the slender elongations of prongs lost in collecting), heavy and solid, presents great variation in shape. Highway, Indio to Coachella, September 30, 1929 (Smiley).

Inset. Gregarious plants imbedded in soil, peridia resting at ground line, fourth sporophore just appearing. Palm Springs highway, California, June 19, 1931 (Clary). $\times \frac{1}{2}$.

PLATE 9

Photomicrograph, vertical section of very young plant in which the columella does not meet the peridium by one cm. Exoperidium broken up into loose ligulate scales. Endoperidium 3–4 mm. thick in growing plant, firm and rind-like. Columella of tough fibrous tissue, with central canal. Glebal chamber filled with soft white pulpy tissue, contains irregular labyrinthine chambers. Walls of chambers roughened by compacted fascicled clusters of basidia. $\times 8$.

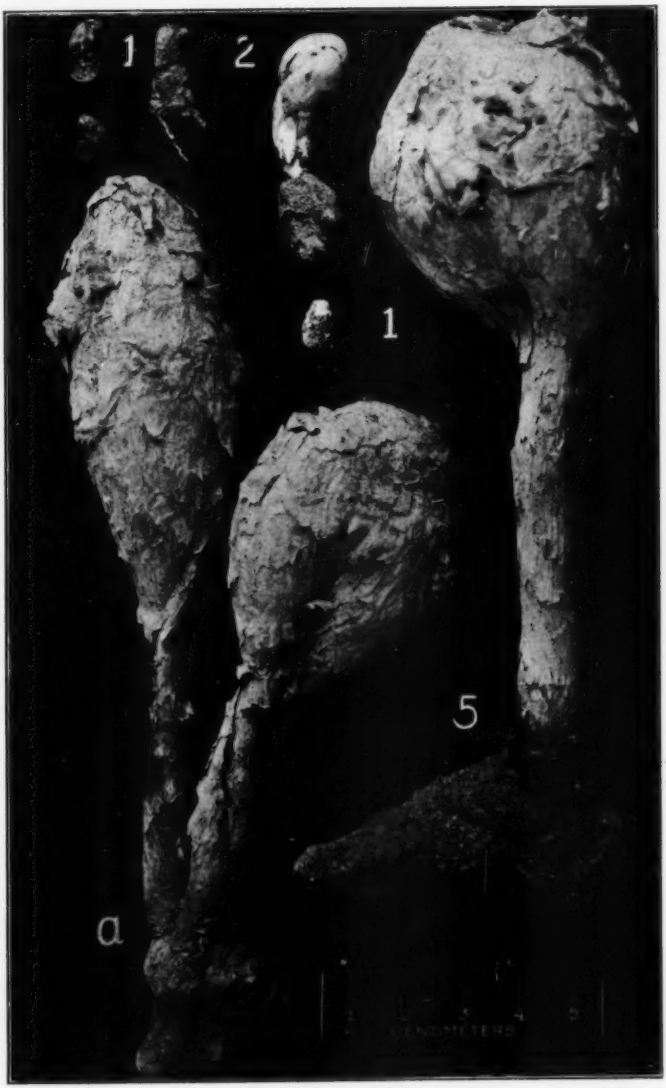
PLATES 10, 11, 12

Glebal tissues in Old and New World material compared.

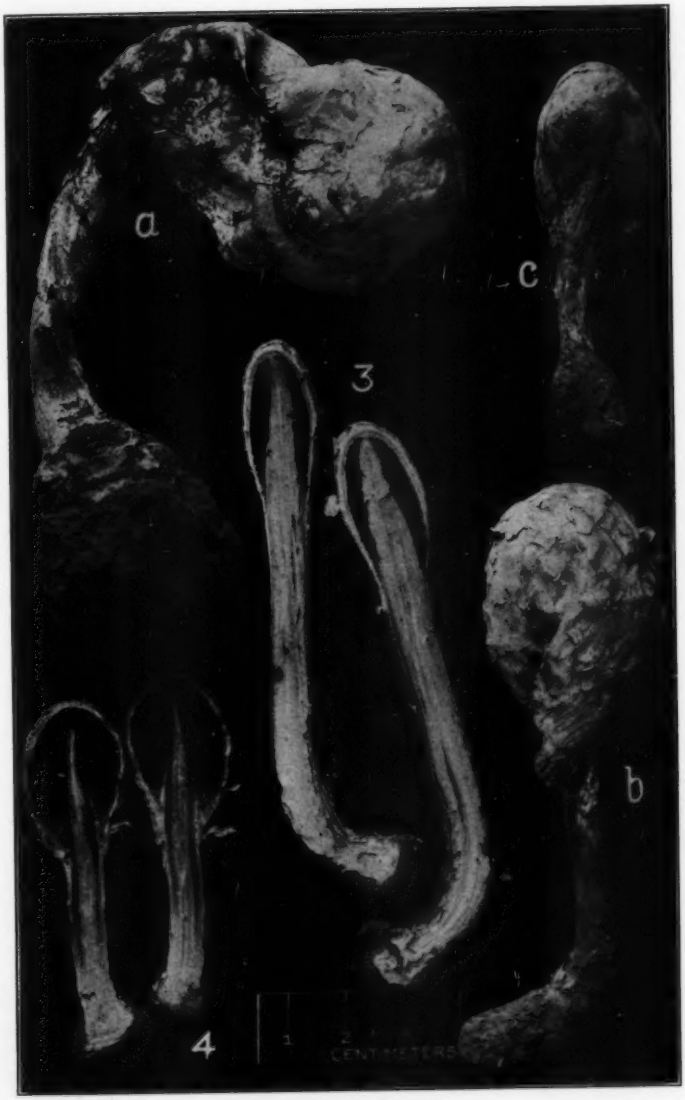
Plate 10, *A*. Spores in Colorado Desert material (Bridwell) show extraordinary variation in proportion and size. Note thick, double walls—the inner deeply colored a rich red-mahogany—also the protoplasmic content, and single germ pore which ends in a circular, hyaline disc by which light is transmitted. Some spores young, devoid of color. $\times 690$.

B. Fascicled, ovoid, hyaline cells—young basidia—large and small, issue from loosely woven ropes of compact hyphae. One large, distended basidium is loose from its cluster (in mount of 50 per cent lactic acid, very rarely seen). Note long, unbranched, colorless threads in this young material (Smiley). $\times 690$. See addendum.

Inset, fig. 1. An average spore in North American material, inclusive of Jamaica (from Thaxter), also of Hawaii (from Shear).



PODAXIS



PODAXIS

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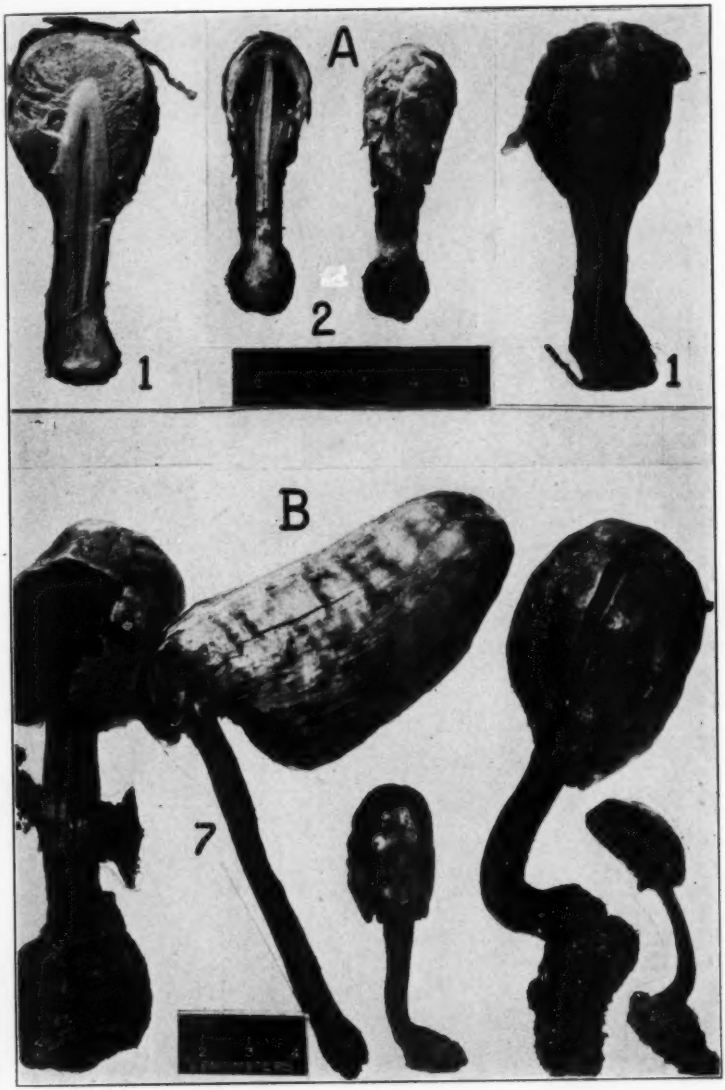

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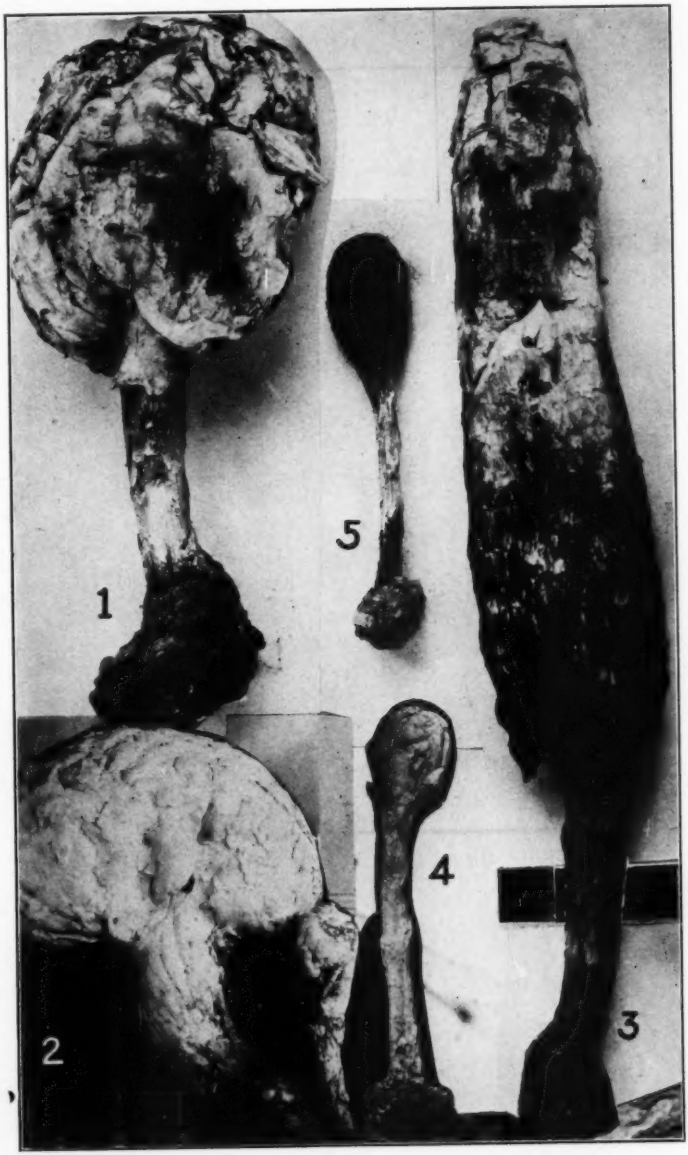

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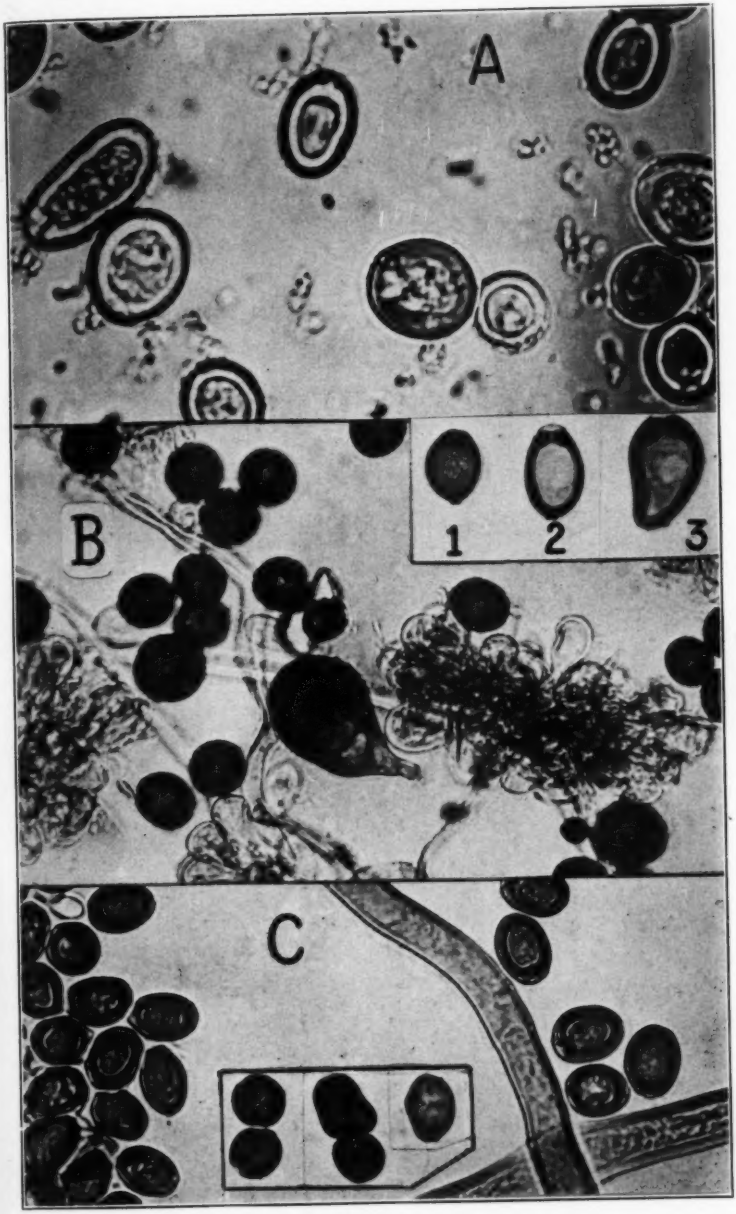

PODAXIS

PODAXIS

PODAXIS

Fig. 2. An average spore in North, West and South Africa, inclusive of islands northwest of Africa (*P. squamosus* Pat.), also of Arabia, *P. arabicus* Pat. (from Maire). Spores show tendency to run broad. See plate 10, *C*, inset.

Fig. 3. An unsymmetrical spore; pear-shaped, constricted at center, or otherwise distorted, may be seen on any slide. See plate 11, *A*, *B*. × 690.

C. Spores and capillitial threads from fully mature material, South Africa (Stephens). Note thick walls of thread, now deeply colored, also thick walls of spores, which show tendency to run narrow. × 690.

Inset. *P. aegyptiacus* Mont. West Sahara (from Maire). × 690.

Plate 11, *A*. Capillitial threads of varying widths, one blind end (rare) lower right. Spores vary in size and shape. Colorado Desert (Bridwell). × 170.

B. One thread, broad, hyaline, flattened and ribbon-like, shows spiral markings and central canal (thread up to 24 μ wide). Note other younger, narrower threads. Spores (borne on fascicled basidia), average broad, show variation in shape and coloration. Jamaica (from Thaxter). × 170.

Inset. Extension of wide thread to the right with opposite twist.

C. Three spiral markings in thread (met "here and there" by Berkeley), from North Africa, *P. aegyptiacus* (from Maire). Spores resemble those in *A* and *B* in size and shape. × 170.

Plate 12, *A*. A single, long, straight, hyaline thread—young—appears in the midst of a mass of fully mature threads. Note uninterrupted central canal. South Africa (from Wakefield). × 190.

B. Capillitial threads fully mature, deeply colored, coil back on themselves rope-like. (All basidia and spores have disappeared.) Walls thick, rather rigid. One thread reveals its spiral structure by separating on lines of striae, showing an open spiral. Note spiral markings in other threads. South Africa (from Wakefield). × 212.

C. Material from South Brazil (from Thaxter) shows precisely the same characters as observed in African material, *A* and *B*, except for the lack of an uncoiled thread. × 212.

ADDENDUM

An illuminating article on the formation of spores in *Podaxis*, from the notes of R. Heim compiled by L. Mangin, comes to hand just as we go to press. It accounts for the extreme variation in size and shape of spores, and confirms the argument presented in this paper that species may not be set off on the basis of the types of variation just named. See Compt. Rend. Acad. Paris **194**: 1182. 1932.

SEPTONEMA TORULOIDEUM: A STAGE OF MYTILIDION SCOLECOSPORUM[1]

MARION LOHMAN

(WITH PLATE 13)

This paper presents a taxonomic and cultural study of *Mytilidion scolecosporum* Lohman (**6**), a species of the Hysteriaceae. The fungus[2] is an exceptionally interesting one, not only because it appears to be intermediary between *Lophium* and *Mytilidion,* showing in some aspects of its life history a rather close affinity with *M. Karstenii* Sacc., but also because it has as a conidial stage the seldom reported Hyphomycete, *Septonema toruloideum* Cooke & Ellis.

SEPTONEMA TORULOIDEUM

Unfortunately, Cooke and Ellis did not publish a complete record of the origin of their imperfect fungus which they described (Grevillea **7**: 6. 1878) as *Septomena toruloideum.* There is, however, a specimen at the Farlow Herbarium labeled in the writing of Ellis, "Septonema toruloidea C. & E. On pine wood. Newfield, N. J. Oct. 17, 1877. J. B. E.," and it is undoubtedly from the original collection. Although it is much weathered, it shows all of the features which are of diagnostic value. There is no necessity of redescribing this material in detail but the following few corrections regarding the configuration of the conidial filaments and additions pertaining to the character of mature conidia, are worthy of record: *conidia deep fuscous throughout or with one or two of the apical cells paler, 3- to 5-septate, 14–18(24) × 4.5–5(6) μ, tapered apically and arranged in simple or sparingly branched, easily broken chains.*

In view of the variation in the size and septation of the conidia within a single member of the hyphomycetous genus, *Septonema,*

[1] Contribution No. 110 from the Laboratories of Cryptogamic Botany, Harvard University.

[2] Collected by Mr. A. H. Smith, from a much weathered stump of *Pinus Strobus* L., at Green Bay, Wisconsin, September 7, 1930.

the material from Wisconsin conforms surprisingly well to the original collection by Ellis. A few differences have been noted: (1) the measurements of the conidia reveal a slightly greater average length as compared with those given in the above emendation, the conidia (FIG. 4) measuring 18–22(25) × 4.5–6 μ; (2) the average number of septa is slightly greater, the conidia being mostly 4- to 5-septate and in a small percentage 6-septate; (3) in the recent collection there has occurred a lesser degree of fragmentation, hence the branching of the filaments is more pronounced, and a greater number of the conidia show paler apical cells. But these are not serious discrepancies since the material, when collected, was in a far less weathered condition than was that collected by Ellis, and since, with the aging of the latter, undoubtedly the filaments have become further fragmented and the paler cells of the conidia have become more deeply colored.

When in a mature but unweathered condition, the filaments (FIG. 5) are erect or variously decumbent, sparingly branched, and measure 75 to 200 μ in length, depending upon the number and size of the conidia. Where the filaments are densely clustered, punctiform centers of sporulation 0.1 to 0.2 mm. in diameter obtain; otherwise, the areas of sporulation are irregularly effused. When in the best of condition, however, the conidial stage is noticeable to the unaided eye only as a blackening of the wood.

It is, presumably, the inconspicuousness of the areas of sporulation which is accountable for the fact that this imperfect stage, so elegant in its habit, has seldom been reported.

Of the few records, that by Ellis and Gerard (**1**, p. 566) [3] and that by Peck (**7**, p. 117) are probably correct, for in each the substratum is the wood of *Pinus*, as it is in the original collection by Ellis and in the collection which initiated this study.

Septonema toruloideum Cooke & Ellis, then, is a taxonomically distinct hyphomycetous fructification occurring probably not infrequently on decaying wood of *Pinus*—and possibly of other coniferous species—in the northern and eastern regions of the United States, and, as the present cultural study indicates, it is to be sought in association with the perfect stage of the fungus.

[3] Written ". . . *toruloides* C. & E." The name *S. toruloides* Berl. undoubtedly stands for another organism.

CULTURAL OBSERVATIONS

Since a *Septonema* (*S. spilomeum* Berk.) had been obtained in cultures of *Hysterium insidens* Schw., in an earlier investigation (**5**), it seemed highly probable that the occurrence of *S. toruloideum* about the hysterothecia of the then unnamed *Mytilidion* was more than a casual association. In verification of the supposed connection, cultural studies were made.

On November 18, 1931, two single asci with their contained germinating spores were isolated. When it was discovered that cultures developing on bacto-cornmeal and on Kauffman's synthetic agar medium (**3**, p. 144) were producing conidial filaments identical with those observed in the field material, additional isolations were made; a number of single germinating ascospores and single asci with intact germinating spores were obtained. Also, culturally produced conidia were sprayed upon plates of the synthetic agar medium and their germination was studied. The conidial development described below is based upon cultures which had originated from single ascospores in the second series of isolations, while the descriptions and figures of mature conidia are based upon the observation of the cultures of the first series.

It was observed in cultures which had originated in the second series of isolations, developing on the synthetic agar medium, that variously oriented, simple or sparingly branched filaments (50 to 100 μ in length) of from five to eight or ten light brown, swollen cells (4 to 6 μ in diameter) had developed by the fifteenth day from the long-celled hyphae of the surface layer. These short superficial hyphae, composed of a number of globular cells, actually chains of initial conidial cells, apparently develop by the successive budding of the distal cells. In their growth, branches arise by the lateral budding of the distal end of any initial conidial cell (but usually of only one or two) in the filament. It was further noted that these filaments of initial conidial cells are transformed into chains of conidia in a more or less regular basipetal manner by the acropetal development of each initial conidial cell. Hence, with respect to a mature conidium, the basal cell is the oldest and each succeeding cell to the distal end of the conidium has followed in order. Exceptions to the acropetal conidial development were observed but the mature conidia, by their shape, color of cells and

variation in the thickness of the wall, generally indicate this manner of growth. It was observed that in the maturation of any one conidium a lateral chain may arise by the lateral budding of any cell of the conidium.

Lateral chains which had arisen during the maturation of a conidium were usually short, being composed of from one to four conidia, while those which had been formed in the development of the filament of initial conidial cells, as already described, were long and conspicuous, maturing four to eight conidia, and more suggestive of the type of branching seen in the field material wherein most of the lateral chains had arisen from apical cells. In these lateral branches, as in the primary conidial chains, the terminal conidium ordinarily is first to mature and is usually the largest. Since a similar sequence in conidial development was found in the cultural study (**5**) of *Septonema spilomeum* Berk., I am inclined to believe that the successive development of conidia from the apex to the base of the filament is common to most of the species of *Septonema*, in spite of the fact that several forms, including *S. spilomeum*, have been illustrated with the larger and apparently older conidia in the basal portion of the filament.

Mature, culturally produced conidia (FIGS. 3, 6) were found to be identical in size, form, color and septation, with those of the field material. They are arranged in fragile chains which are supported by conidiophores, 20 to 50 μ in length, composed of a variable number of yellow to brownish cells, 2 to 3 μ in diameter (FIG. 6). The conidia germinate readily by a single cylindrical tube from each of the terminal cells (FIG. 3) and, occasionally, by a similar tube from any one of the central cells.

In the study of the germinating conidia it was noticed that the germ tubes of morphologically immature conidia ordinarily form first a series of short swollen cells in a manner which has been described and figured (**4**) for immature ascospores in certain species, and for apparently mature ascospores in other species, of the Hysteriaceae.

Although a pycnidial stage was found to be the usual type of secondary sporulation in the species of the Hysteriaceae which I had previously investigated (**5**), all efforts to induce the production of pycnidia in the cultures of this organism have been unsuc-

cessful. In its vegetative cultural characteristics the organism is scarcely distinguishable from a form which I have referred (**5**) to *Mytilidion laeviusculum* (Karst.) Sacc. It is only upon the production of the numerous conidial chains that the superficial layer in the cultures becomes more pronounced than that in the cultures of *M. laeviusculum*.

The cultivation of *M. scolecosporum*, then, from isolated germinating ascospores and isolated asci with their contained spores, has shown the associated hyphomycetous stage, identified as *Septonema toruloideum* Cooke & Ellis, to be a stage of that fungus. The cultural study has revealed the manner of conidial development, which is a rather complicated process, probably common to most of the species of *Septonema*, and one that has not previously been adequately described on the basis of growing material. The knowledge of the general mode of conidial production and the observation of exceptions to the rule, in culture, enable one to interpret more satisfactorily in the study of field material the various degrees of branching, the number of conidia in a chain and the number of septa in a conidium, all characteristics of taxonomic import, variations of which certainly obtain in the conidial sporulation of the organism under fluctuating field conditions. Particular attention has been given herein to this hyphomycetous stage because I am convinced that it will be through our knowledge of the imperfect stages that better specific and generic concepts in the Hysteriaceae will be achieved.

IDENTITY OF THE ASCIGEROUS STAGE

Mytilidion scolecosporum has been described in a previous paper (**6**). It is important, however, in inquiring into the probable affinities of the species that its diagnostic features be reviewed.

The dull black, longitudinally striate, aggregated fructifications are conchiform but not acutely keeled and measure 0.4–0.8(1) $\times$ 0.2–0.3 mm. They conform well to Karsten's (**2**, p. 245) original description of his *Lophium mytilinum* (Pers.) Fries. But, when compared with Karsten's distribution under that name and with the specimens of *Mytilidion rhenanum* Fuckel (*956*. Ex Herb. Fuckel. 1894) in the Farlow Herbarium they resemble more closely those under the latter name. They are in places sur-

rounded by the effused black crust of the *Septonema* stage. (Even Karsten noted (*l.c.*), "Perithecia plerumque e crusta late effusa. . . ."

The asci measure 100–130 × 4–5.5 μ, being somewhat smaller than those originally described by Karsten (**2**, p. 245) for what is now known as *M. Karstenii* Sacc., and they are accompanied by delicate, septate paraphyses which are sparingly branched and interwoven above. The paraphyses resemble those commonly encountered in species of *Mytilidion* more than do the still more delicate sterile filaments seen in species of *Lophium*.

As to the spirally biseriately arranged ascospores, they are elongated, subvermiform, occasionally bent or subsigmoid, 5- to 7-septate, yellow to clear brown, and measure 40–50 × 2–2.5 μ. The ascospores are slightly longer and not as broad as those described by Karsten. They are figured here (FIGS. 1, 2) with those of Karsten's "Fung. Fenn. *93*," in which the 3- to 4-septate spores measure 31–37 × 3.5–4 μ, being smaller than the 3- to 7-septate spores described by Karsten (**2**, p. 245) as measuring 34–45 × 4–5 μ. Although it was noted that the hysterothecia of the new form resembled closely those of *M. rhenanum* Fuckel, the 3- to 5-septate spores of the latter are still smaller, averaging 28–32 × 3.5–4.5 μ, agreeing more or less with Rehm's conception of that species.

Rehm (**9**) retained both *M. Karstenii* Sacc. and *M. rhenanum* Fuckel, in spite of their intergradation. Previously (**8**), he had noted that the former is a species intermediate between *Lophium* and *Mytilidion*. As the comparative data related above indicate, *M. scolecosporum* shows a probable close relationship with these two species but stands apart in that the ascospores are both longer and narrower than those of *M. Karstenii* Sacc. There is to be considered, however, the evidence contributed by the conidial stage; evidence which indicates a possible close affinity of this scolecosporous form with *M. Karstenii*, thus supporting Rehm's (**9**) contention that in these forms we should not place too much emphasis on the character of the ascospore.

In 1886, Dr. Thaxter collected (at Kittery Point, Me.) a form on *Pinus* which he determined to be *M. Karstenii* Sacc. Its ascospores are yellowish to clear brown, 3- to 7-septate with slight

constrictions at several of the septa, tapered only slightly toward the upper end, and measure 38–49 × 4–4.5 μ. The specimen in the Farlow Herbarium represents very well the fungus which Karsten adequately described (2, p. 245). I find a much weathered *Septonema* stage associated with the hysterothecia. In it the conidia are deep fuscous, 3- to 5-septate, and measure 18–30 × 6–7 μ, not exceeding greatly the measurements given herein for *Septonema toruloideum*. Again on *Pinus* but unaccompanied by a conidial stage, Dr. Farlow (at Shelburne, N. H.) collected the fungus in 1891. From the two collections of *M. Karstenii* that were made in New England, *M. scolecosporum* differs primarily only in its narrower ascospores.

The evidence is convincing that we have in this country a fungus very similar to that described by Karsten as *Lophium mytilinum* (Pers.) Fries, now known in Europe in divergent forms as *Mytilidion Karstenii* Sacc. Also, that we have a species, probably closely related to *M. Karstenii*, which is apparently intermediary between *Lophium* and *Mytilidion* and which perhaps is continuing largely by means of its conidial sporulation.

Likewise, the evidence is convincing that cultural studies, supported by the observations on associated conidial stages, will be necessary to a correct interpretation of the affinities of certain American and European species which appear on the basis of our present taxonomic system to be intermediate between *Lophium* and *Mytilidion*.

SUMMARY

This paper presents a taxonomic study of *Septonema toruloideum* Cooke & Ellis and the cultural evidence which establishes this long-known but seldom reported Hyphomycete as a stage of the recently described hysteriaceous fungus, *Mytilidion scolecosporum* Lohman. The original description of *Septonema toruloideum* by Cooke and Ellis is corrected on the basis of an examination of authentic material and some new light is thrown on the relative value of diagnostic characters in the hyphomycetous stages referable to *Septonema*, by the observations on the mode of conidial development in the pure cultures of the hysteriaceous fungus.

The two types of lateral conidial chains, as determined by their time and place of origin, are described as well as the manner of development of the filaments of initial conidial cells, the formation of mature conidia from single initial cells, and the sequence in the maturation of these cells in the development of conidial chains. The processes are described in some detail in view of their bearing on the identification of species of *Septonema* and in view of the lack of developmental studies in the literature on members of this form genus.

Particular attention is given to the hyphomycetous stage because of the conviction that a better understanding of specific and generic relationships in the Hysteriaceae will be reached through a careful study and proper emphasis of their imperfect stages.

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EXPLANATION OF PLATE 13

As reduced, all drawings except those of the last two figures represent an approximate magnification of 1350 ×. The true magnification, as well as the actual measurements of the materials figured, are determinable from the absolute scales shown. The scale for fig. 3 also applies to fig. 4.

Fig. 1. Germinating ascospores of *Mytilidion scolecosporum*. The one spore, by its two inactive cells, shows clearly the degree of swelling.

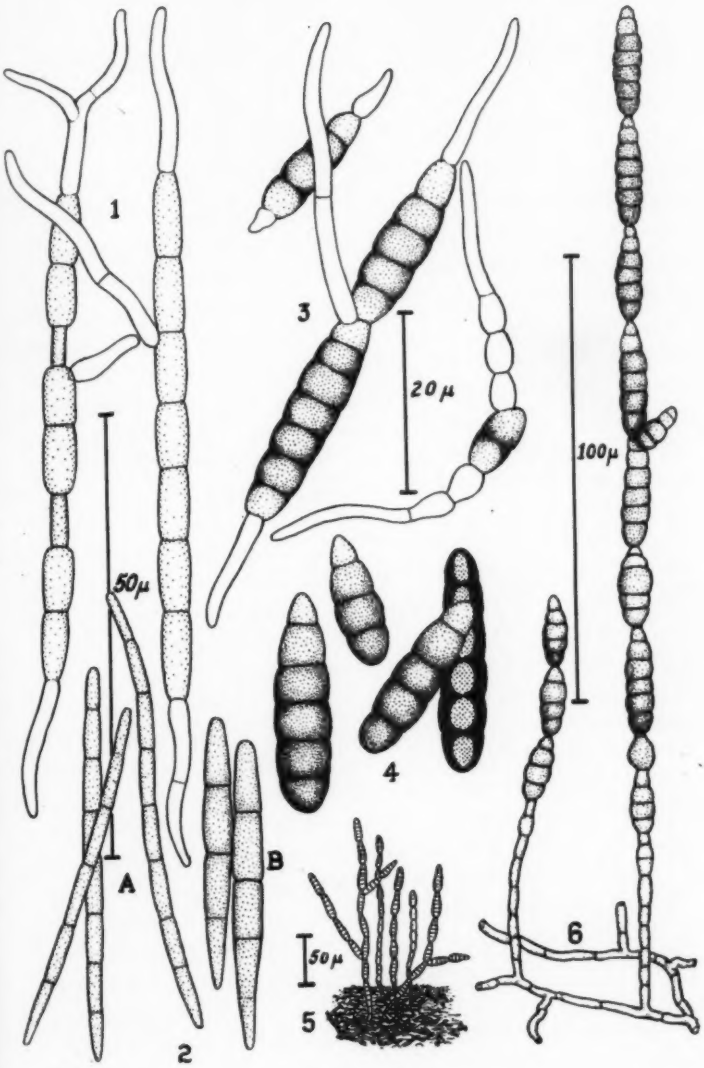
Fig. 2. *A*. Typical ascospores of this species as they appear when mounted in water and examined immediately. *B*. Two ascospores of *Mytilidion Karstenii* Sacc. as Karsten's specimen, "Fung. Fenn. *93*," represents the species. The slightly longer spores described in the text for another American collection which also has a *Septonema* in association, are of the same general character but conform more closely to those upon which Karsten's original description was based.

Fig. 3. Conidia which were obtained in a pure culture of the fungus and then germinated upon a synthetic agar medium. The 4- to 6-celled conidia illustrated in this figure (and in the last) typify the mature conidia obtained in cultures which had originated in the germination of the ascospores of isolated asci.

Fig. 4. Mature conidia of the hyphomycetous stage which was associated with the perfect stage of the fungus and which proved to be *Septonema toruloideum* Cooke & Ellis.

Fig. 5. A habit sketch of several conidial filaments; based upon the associated imperfect stage and an authentic specimen of *S. toruloideum* Cooke & Ellis. The present magnification is approximately 137 ×.

Fig. 6. Two of the numerous conidial filaments which were observed in the pure cultures that had originated in the manner noted previously in the legend for fig. 3. In these cultures the degrees of branching illustrated in fig. 5 were again observed. Approximately, × 675.



MYTILIDION

FURTHER STUDIES IN NEUROSPORA SITOPHILA

ALICE ARONESCU

(WITH PLATE 14)

It is known from Dodge's studies of *Neurospora* (1930) that if you cross an albinistic (non-conidial) strain of *N. sitophila* with a conidial strain you obtain perithecia with asci whose progeny present the conidial and the sex [1] characters as segregated in a perfect Mendelian ratio.

We shall discuss below our results in the study of this segregation in connection with the two opposite interpretations, that of Dodge (1931, 1932) on the one side, and that of Moreau and Moruzi (1931) on the other side, regarding the nature of the phenomenon which induces the formation of perithecia with asci.

SEGREGATION OF CONIDIAL FACTORS IN U-TUBE PERITHECIA

In a recent paper Dodge (1931) reports the results obtained in experiments concerning the formation of perithecia in U-tubes. Modifying the Moreau-Moruzi experiment he grows, in most of the cases, an orange-colored conidial race, for example, either 56.7 or 56.8 in one arm of the tube and an albino race, either 56.1 or 56.2 in the other arm. We shall not give here in detail the results and their interpretation, but shall merely mention that after careful observations regarding the growth of the mycelium in the two arms of the tube as well as regarding the place and conditions necessary for the formation of mature perithecia, the author concludes that "hypothetical diffusible hormones, if any are produced by the strains of *Neurospora sitophila* and *N. tetrasperma* cultured, are not potent to induce the formation of perithecia with asci in U-tube cultures such as were described by Moreau and Moruzi."

For the purpose of verifying in another manner the value of

[1] The term sex is used for convenience to indicate that two mycelia which must be grown together to produce perithecia behave as though they were of opposite sex.

this " hormone theory," we undertook to analyze the asci from the perithecia obtained by Dodge in some of his U-tube experiments.

In the analysis of the spores of these asci we could expect the following three alternatives:

1. We may suppose with Dodge that for the maturing of a perithecium an act of fertilization is necessary, that is, there must be a fusion of nuclei derived from hyphae of the two strains. In that case, whether the perithecia are obtained from the arm of the tube with + C strain, or from that with — C strain, we should find in all the analyzed asci, a segregation of sex and conidial factors in a perfect Mendelian ratio.

2. Corresponding to the conclusions of Moreau and Moruzi, namely, that there is at the basis of fertile perithecia no act of copulation and therefore no exchange of nuclei, but that it is all the result of the action of diffusible hormones, we should then find, if the perithecia were found in the arm with the + C strain, that all the spores from any of the asci would give conidial strains with the same " sex " as strain + C. If, on the other hand, the perithecia are formed in the arm with the — C strain, all the eight spores from every one of the asci must give albinistic strains like the — C strain.

3. Let us consider a third possibility as suggested by Dodge (1931), namely, that contrary to all our present conceptions, the genes for the Mendelian inheritance of morphological characters are also diffusible hormones. We would then expect to find, as long as we know that there is no linkage between the sex and conidial factors (Dodge 1929, 1930) that the genes of these characteristics also should work separately and at random. In the analyzed perithecia we should then find, also at random, three categories of asci. In an arm where at the beginning we had, for example, a + C, " sex " B strain, we might find all eight spores + C, four sex A and four sex B; or we might find all eight spores of the same " sex," four + C and four — C; or in the third case a Mendelian segregation according to the first alternative given above. Presupposing that the perithecia are formed in a — C and " sex " B arm, there would still be, correspondingly, three other possibilities.

MATERIAL AND METHOD

The chosen material was as we have already mentioned, mainly from asci obtained by Dodge (1931) in his U-tube experiments. Aside from these cultures there were also analyzed other perithecia produced from inoculations made by the writer on corn meal agar U-tubes which served in the studies concerning the second question presented in this paper, the description of which is given in that part.

From Dodge's material we analyzed at random thirty-seven asci representing nineteen perithecia from eight U-tubes, and from our own material thirteen asci developed in six perithecia from five U-tubes.

For the germination of the spores and the derivation of strains we used the methods as described by Dodge (1928, 1930).

In this connection we should mention that the spores of some of the cultures kept in the ice box for some time for the purpose of checking the shooting of the ascospores, germinated with great difficulty and in a much lower percentage than those subjected to the usual conditions.

As a matter of fact the number of analyzed asci was much greater than fifty. We, however, took into consideration for this report, only the results from the asci which had at least five germinated spores, so that one of them could be different from the others, had any segregation taken place. In the case of three asci, where only four and three spores respectively germinated, the results were taken into consideration in as much as the germinated spores were of two kinds as to their factors for conidia.

The spores of twenty-five asci were separated in order so that the position of each spore in the ascus was known. Those of each of the other twenty-five asci were isolated without any order as to the position in the ascus. From among the first group we obtained five complete sets of eight germinated spores. From five other asci, cultures from seven spores each were obtained. From the remainder except for two asci with four and three germinated spores respectively, cultures from either six or five spores were obtained. From the asci the spores of which were isolated at random, we obtained, in eight cases, entire sets of eight germinated

spores, several sets with seven and six spores, a few with five each and one single case with four spores.

In all fifty asci, without a single exception, whether the spores were isolated in order or not, we observed segregation of sex and conidial characters in a perfect Mendelian ratio. Since a conidial strain, + C, was always grown in one arm of the U-tube and a non-conidial strain, — C, in the other, and both of these contrasted characters showed in each ascus, nuclei from each strain must have in some way come together in each ascus.

Wilcox (1928) found the sex factors segregating at the second division in the ascus. Subsequently it was determined that sex factors and conidial factors segregate independently (Dodge, 1929, 1930; Lindegren 1932) either at the first or the second division. Among the group of asci whose spores were isolated in order, "sex" factors were segregated at the first division in thirteen cases, and at the second division in the other twelve cases. The conidial factors were segregated at the first division in twenty-one cases and at the second division in only four cases.

We also found eleven cases where both sets of factors segregated at the first division and only two cases in which both sets of factors segregated at the second division.

The perfect segregation obtained with all the described cases, leads us naturally to the conclusion that the hormone theory of heterothallism in *Neurospora* announced by Moreau and Moruzi, has not been borne out in our experiments.

RATE OF MYCELIAL GROWTH AS RELATED TO SEX AND CONIDIAL CHARACTERS

In the studies concerning segregation of sex and conidial factors in *Neurospora*, previous authors have shown that there is no linkage between those two characters.

Lindegren (1932) in his paper on inheritance of response to heat treatment in *Neurospora* finds that in the case of *N. tetrasperma* the spores seem to respond in a rather uniform manner to heat treatment. He also finds that the small variations presented by *N. crassa*, after one hour of heat treatment, are possibly due to genetic factors. In the case of *N. sitophila* and of a certain hybrid, he finds two kinds of ascospores in respect to their response to heat

treatment. Due to the many variabilities observed, the author is in doubt as to whether this character could be considered in the genetics of *Neurospora*. He also does not find any obvious connection between this character and the sex and conidial characters.

Along the same line of thought the question arises as to whether another physiological character, namely "rate of growth," could not be constant and be represented by factors which segregate like the sex and the conidial factors, being possibly linked to one of these.

In a recent paper Moreau and Moruzi (1931) find a difference in rate of growth between the two mycelia of their conidial races of *Neurospora*. One is of French origin and "sex" B and the other one of American origin and "sex" A. They found that the "sex" B strain grew the more rapidly.

METHOD OF PROCEDURE

Two strains of different sexes were grown in one arm of a corn-meal agar U-tube; the medium in the other arm was not inoculated. The grouping of the pairs was made in such a way as to obtain all the possible fertile combinations among the strains derived from the same ascus. In this manner three different categories of crossings were possible, between $-C$ and $+C$, between two $+C$ strains and between two $-C$ strains. It is evident that only one fertile combination could be made among those strains from ascospores formed in an ascus where segregation of conidial and sex factors took place at the first division.

It was made certain that the cultures used in the experiment were not old and that they were of about the same age. In all, eighty-six U-tube crossings were made.

At first, the surface of the agar in the arms of the U-tube was inclined. Afterwards it was changed to level, and was so maintained during the remaining series of experiments. The cultures were kept in an incubator at a temperature of about 25° C.

After an interval of from three to five days, perithecia were formed at the surface of the inoculated agar, while after six to ten days after inoculation, one of the mycelia of the two strains appeared at the surface of the agar in the second arm. This variation in time was due to the difference in lengths of the columns of

agar through which the mycelia traveled. The position of the growing mycelium in the agar could be observed and marked every day with the aid of a magnifying glass.

As soon as the first mycelial hyphae appeared at the surface of the second arm, transfers were made to a separate test tube. They were allowed to develop and the strain was finally tested for sex, being grown separately with each of the two strains from the first arm or with each of two albinistic strains, 56.6 " sex " A, and 56.1, " sex " B, used as tester strains. Having found in this manner the sex of the strain which arrived at the surface of the second arm, it was definitely established which of the two strains inoculated in the first arm grew the faster. For the purpose of eliminating any uncertainty it must be mentioned that as soon as one of the strains begins to grow downwards, toward the connection arm of the U-tube, the growth of the second strain is entirely checked.

Each series of U-tubes was very carefully observed through a period of one month. In not a single case did any perithecia form at the surface of the second arm. This means that in no case were both strains able to arrive at the surface of the agar in the second arm.

After varying intervals of time the agar in the two lateral arms of the U-tube began to dry, and air pockets appeared against the glass. In most cases the first pocket formed was that in the arm where the two strains had been inoculated. Even though the two mycelia were later found in this first air pocket, nevertheless, there was rarely found examples in which they formed perithecia in this region. It is probable that most times and especially when a greater interval of time had passed until pockets began to form, the mycelium which had grown more quickly towards the surface of the agar of the second arm of the U-tube was too old to take part in fructification.

Most frequently, after the appearance of one of the strains at the surface of the agar in the second arm, air pockets began to form there as well. During this time branches from the mycelium which had arrived at the surface had grown backwards along the column of air and as soon as the two pockets joined in the connecting arm, the two mycelia met. In the usual interval of time perithecia were formed in this space, beginning in the con-

necting arm and continuing for some distance along the arm of the tube where inoculations had been made.

We should add that of the eighty-six tubes experimented with, one whole series of eleven which were poured and inoculated on the same day, behaved, at the beginning, differently from all the others. In all these cases the growth of the mycelia was checked almost immediately after the formation of the perithecia. These tubes were kept under observation from February 9 to March 28 during which time one could easily see, by the aid of a magnifying glass, that the mycelia remained completely stationary. On March 28th, with the aid of a sterile probe, the agar column was separated all around from the glass as far down as the length of the probe allowed it. Air pockets could then be seen against the tube walls and after from four to eight days, one of the two strains in every one of the tubes appeared, as usual, at the surface of the agar in the second arm.

The importance of the presence of air in the formation of perithecia and the growth of the mycelium through the agar is shown by Dodge in a recent paper (1931), and Dr. F. L. Denny of the Boyce Thompson Institute has recently reported before the Torrey Botanical Club (Torreya **32**: 138. 1932) further important contributions on oxygen requirements.

RESULTS OBTAINED

In our observation, the aim was to find, as already mentioned above, whether there is a linkage between factors for "rate of growth" and factors for condia or for sex. The results show that no linkage can be established between those characters. It is quite apparent that the preponderance of growth of one of the strains depends upon no set rule and that it is probably very largely determined by the conditions in the medium. See plate 14.

It was at first thought that the inclined surface of the agar might give rise to errors in the interpretation of the results for the reason that the conditions for the growth of the two strains were not equal. The same inoculations repeated on level surfaces did not make any difference in results. The same pair of strains, crossed several times in different series of experiments, behaved differently. Even if it may have appeared at times that one of the

strains of the pair had a more rapid rate of growth, nevertheless the variations noted from all the results were so numerous, that it was necessary to conclude that the " rate of growth " is not a characteristic linked either with sex or with conidial factors. Two strains of different sexes, on the one hand, or an albinistic and a conidial strain on the other, do not seem to be constantly different as regards " rate of growth." Still, we cannot overlook the question as to whether " rate of growth," without being linked to the other characteristics, may not be a fixed character represented by genes which could segregate independently. Our experiments do not tell enough in this connection. Other conditions are required in which all the strains from an ascus should be cultivated comparatively in separate U-tubes under identical conditions and through several generations.

SEGREGATION OF " SCLEROTIUM " FACTORS IN ALBINISTIC STRAINS OF NEUROSPORA SITOPHILA

The presence of sclerotia, bulbils or incipient perithecia in cultures of *Monilia sitophila* is mentioned by several authors (Dodge 1930, 1931; Moruzi 1930).

During our experiments, mentioned above, concerning segregation in U-tube perithecia, while analyzing the asci formed by mating two albinistic strains, we found in two successive cases two complete sets in which four of the albinistic strains showed a great abundance of incipient perithecia (" sclerotia "), while the other four had very few of these bodies. The great difference between the number of bodies was very evident. The four strains rich in these structures have a grayish-black appearance, while those with the very few, still show frequently the yellow color in the tufts of the aerial hyphae.

For the purpose of facilitating the explanation of what is to follow, we shall designate the strains with few incipient perithecia by " s " and those strains with large number by " S."

After having determined the sex of each of the cultures, crossings were made between strains of opposite sex, one being " s " and the other " S." Complete sets of spores from two asci were isolated and grown. These were second generation and showed again the characteristics " s " and " S " separated in the same

manner and perfectly distinct. Tried again for sex on a different lot of corn-meal agar medium it was noted that the sex factors segregated independently without any relation to the sclerotial condition.

By making transfers of these strains of the second generation still on corn meal agar, the differentiation did not manifest. The same transfers were then made to potato-dextrose agar with pH = 5.6 and dextrose agar with pH = 7.5. The differentiation appeared again very definitely. The fact that this character did not behave uniformly in all the transfers, might be due to one of two alternatives; either this is a character that is not constant or, if it is, it does not appear with every cultural condition, because it might be influenced by the composition of the medium and by its pH. New experiments were carried out to obtain further information on this question.

METHODS

We should mention here that in the two sets of strains, regarding which we spoke above and which we continued using in our experiments, the cultures were marked in the following manner:

In one of these, the spores were numbered from 1 to 8 being isolated in the order showing their position in the ascus. In the second set the cultures were distinguished by letters a to h, the spores being isolated at random from that ascus. In the first set the strains 1 to 4 were those with numerous incipient perithecia, "sclerotia" ("S"); while numbers 5 to 8 had few "sclerotia" ("s"). From the second set, strains a, e, f, d, were "S" and b, h, g, c, were "s."

Both series of cultures were transferred to four kinds of media which were in turn changed to four different pH values, approximately 5.4, 6.4, 7.4 and 8.4. Two identical series of experiments were run at different times.

We give below the media with their respective formulas

CORN MEAL AGAR. Extract from 40.1 gr. corn meal at 60° C., for 1000 cc. of medium.

DIFCO POTATO DEXTROSE AGAR. (A preparation containing infusion from dried potatoes, bacto dextrose, bacto agar.) 40 gr. for 1000 cc.

DIFCO BACTO DEXTROSE AGAR. (Containing bacto beef extract, bacto peptone, bacto dextrose, bacto agar.) 33 gr. for 1000 cc.

CZAPEK'S SOLUTION AGAR. (After Thom; 2.0 gr. sodium nitrate, 1.0 gr. potassium phosphate, 0.5 gr. magnesium sulphate, 0.5 potassium chloride, 0.01 gr. ferrous sulphate, 30 gr. sucrose. 1000 cc. distilled water.)

The entire lot of medium necessary for one series of experiments was made at the same time. The pH was afterwards changed by adding, according to need, HCl or NaOH in N/10 solutions. The pH was checked, for the acid media, with the aid of indicators bromocresol purple and chlorophenol red in solutions of 0.04 per cent, and with phenol red and cresol red 0.02 per cent for the alkaline media. For comparisons we used the chart of indicators from the 3d edition of W. M. Clark's manual "The Determination of Hydrogen Ions." It is apparent that the method used permits but rough comparisons. We may pass over, however, the possible experimental errors involved, considering them as relatively unimportant as regards the results obtained in the growth of the fungus.

RESULTS OBTAINED

On corn meal agar the segregation appeared very distinct. The strains "S" had a dark gray color with inumerable "sclerotia" giving the medium a blackish appearance. Strains "s" presented light pink tufts of mycelium and very few "sclerotia" were visible to the naked eye. These contrasted differences were relatively the same in all of the cultures, irrespective of the pH of this medium, showing that the pH factor, so far as varied in this experiment, does not bring about any change in their general aspect.

On potato dextrose agar the segregation also appeared, but not as definite as on corn meal agar. An abundant mycelium was present in all the strains. The "S" cultures had again the large number of "sclerotia" but giving the medium a brown-blackish appearance. The "s" strains had fewer of these bodies turning the medium to a dark reddish-brown color. The variations in the pH gave rise here to small differences, the color shades of the media became lighter with the increase in acidity.

On Czapek's solution agar the difference was again very ap-

parent. Strains "S" presented numerous "sclerotia" and quite abundant mycelium. Cultures "s" did not have any of those bodies as far as could be seen with the naked eye, while the mycelium was poorly developed. There were no perceptible differences brought out by the changes in pH.

On the dextrose agar, irrespective of the pH, the mycelium of all the strains is very abundantly developed, presenting at the upper part of the culture rich tufts of yellowish color. Very few perithecial bodies appeared, therefore the segregation was not visible.

These results may be interpreted as follows:

Recent studies (Dodge, 1932) have confirmed the opinion that these organs are incipient perithecia. By spermatizing these incipient organs of a strain of one "sex" with monilioid conidia or with microconidia from a strain of the opposite "sex" mature perithecia with ascospores were obtained.

Having this in view, we are able to explain why the segregation of the factors for this character continues to be incomplete during two generations. As long as we assume that these organs are incipient perithecia, we cannot ever expect a complete segregation, unless the production and the function of these receptive bodies is controlled by several pairs of factors or is an indication of femaleness.

The constant character obtained by us should be then interpreted in the sense that some strains are capable of greater fructification and form, therefore, more incipient perithecia, while others are less fruitful and form fewer receptive bodies.

SUMMARY

1. Our experiments lead to the conclusion that the theory proposed by Moreau and Moruzzi concerning hormone responsibility in the formation of mature perithecia in *Neurospora sitophila,* is untenable.

2. Rate of mycelial growth in *N. sitophila* is not linked to sex or conidial characters and seems to be greatly influenced by environmental conditions. This is not to deny that certain strains may not have an inheritently high rate of growth or vice versa.

3. In a mating of albinistic strains of *N. sitophila,* we observed

in the same ascus the separation in an uniform and constant manner of characters " S " and " s."

The incomplete segregation obtained, strengthens the assumption that these organs are incipient perithecia.

4. It is obvious that the appearance of " sclerotia " or incipient perithecia depends on the composition of the nutrient medium, but is not much influenced by the pH factor.

This work was done at The New York Botanical Garden under the direction of Dr. B. O. Dodge to whom I wish to express appreciation for suggestions and criticisms. I am also indebted to Miss Marjorie Swift, for the necessary culture material which was placed at my disposal and for many other courtesies.

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Left. Race 56.3, conidial and sex B, grew faster than race 56.6, nonconidial and sex A. Right. Race 56.7, conidial and sex A, grew faster than 56.2, nonconidial and sex B. Here the conidial races grew faster in both cases than did the nonconidial races. No sex linkage.

PHOTOGRAPHS AND DESCRIPTIONS OF CUP-FUNGI—XVIII. RARE SPECIES OF GODRONIA [1]

FRED J. SEAVER

(WITH PLATE 15)

The genus *Godronia* was established by J. B. Mougeot in 1845 who characterized it as having apothecia which are coriaceous or gelatinous but with the spores of a *Stictis*. While typically the spores of the genus are filiform the limits have been somewhat extended to include those forms in which the spores are much elongated and fusiform. It is difficult to segregate arbitrarily on this basis. Hence a number of species have been included which might appear to belong elsewhere. The genus overlaps *Scleroderris* of the Phacidiales so that some of the species have been used interchangeably between the two and in fact it has been suggested by some mycologists that the genera are identical.

During two collecting trips to Colorado among other collections the writer obtained two rare species of the genus *Godronia*. The first of these has been twice described as new first by Ellis and Everhart, later by the writer but is now found to be synonymous with an old European species, as brought out in the accompanying treatment. The second has been extensively known in this country in its conidial stage but does not seem to have been so commonly collected in its perfect form. For these reasons it is thought well to describe and illustrate the two species giving our present conception of their synonymy. Both have been found accompanied by their conidial stages which adds interest to the problem.

SCLERODERRIS FULIGINOSA (Fries) Karst. Myc. Fenn. **1**: 216. 1871.

Sphaeria fuliginosa Pers. Obs. Myc. **2**: 68. 1799.

Cenangium fuliginosum Fries, Elench. Fung. **2**: 23. 1828.

[1] This paper is preliminary to a monograph of North American Cup-fungi (inoperculates), a companion volume to North American Cup-fungi (opercu-lates), which was published by the author and issued in December, 1928.

Lasiosphaeria striata Ellis & Ev. Proc. Acad. Sci. Phila. 1893: 443. (1894?)

Godronia Bethelí Seaver, Mycologia **3**: 64. 1911.

Godronia striata Seaver, Mycologia **4**: 123. 1912.

Apothecia erumpent through the outer bark, of the host, single or occurring in clusters, often so numerous as to form congested masses many cm. in extent and often almost entirely surrounding the branches on which they grow, the individual apothecia at first nearly globose, opening at the top so as to leave an irregular margin, at maturity about 1 mm. broad and the same in height, brownish and furfuraceous externally and longitudinally striated; hymenium whitish or bluish-white; asci clavate, reaching a length of 130 μ and a diameter of 7–8 μ, 8-spored; spores fasciculate in the ascus, subfiliform, tapering toward either end, sharp-pointed, 3–4 $\times$ 65–85 μ, becoming 7-septate at maturity and often slightly constricted at the septa, hyaline; paraphyses abundant, filiform.

Pycnothecia often accompanying the apothecia at first closed becoming shallow cup-shaped, usually black; pycnospores fusiform, straight or slightly curved, 3-septate, 3–4 $\times$ 28–30 μ.

On branches of *Salix*.

TYPE LOCALITY: Europe.

DISTRIBUTION: Ontario and Colorado; also in Europe.

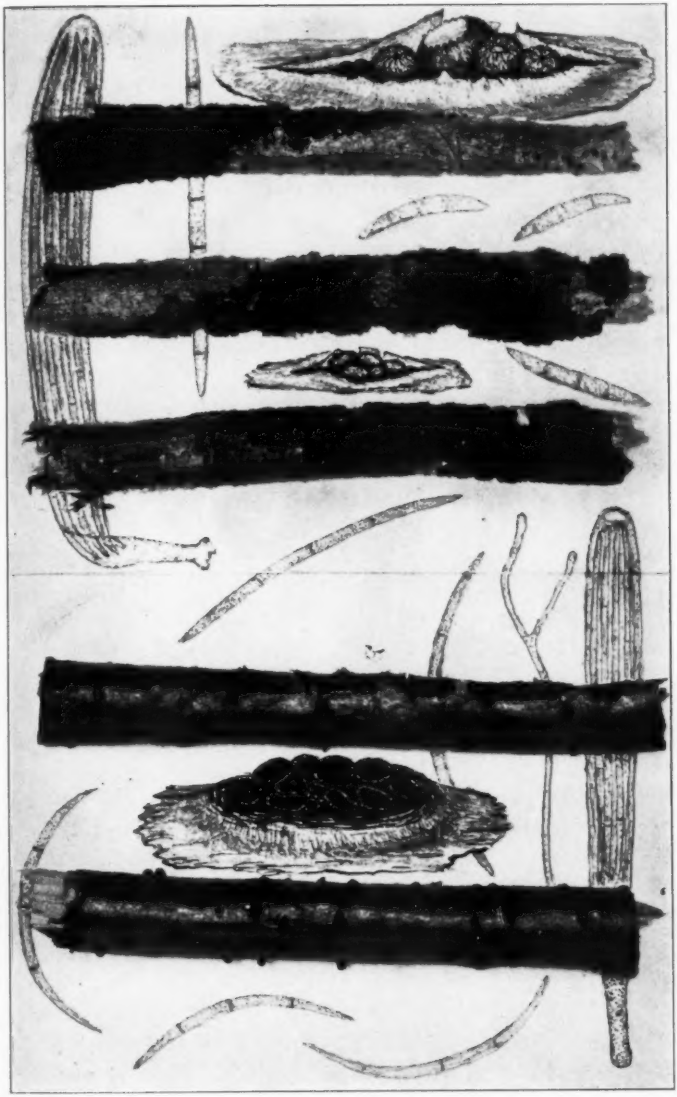
ILLUSTRATIONS: Tul. Fung. Carp. **3**: *pl. 20, f. 1–4;* E. & P. Nat. Pfl. **1**[1]: 255, *f. 187, H–J*.

This species was collected in abundance on willow at Tolland, Colorado by the author in company with Ellsworth Bethel in 1910 and described as a new species, *Godronia Bethelí*. Later study revealed the fact that *Lasiosphaeria striata* Ellis & Ev. is identical but owing to the fact that it had been placed in the Sphaeriales it had been overlooked. The young apothecia are strongly constricted which doubtless accounts for the fact that Ellis placed it in that group. Recent study has revealed the fact that both Ellis & Everhart's species and the species of the writer are identical with *Cenangium fuliginosum* of Fries.

SCLERODERRIS SERIATA (Fries) Rehm, in Rab. Krypt., Fl. **1**[3]: 211. 1899.

Cenangium seriatum Fries, Syst. Myc. **2**: 185. 1822.

Phacidium seriatum Fries, Elench. Fung. **2**: 131. 1828.



GODRONIA FULIGINOSA
GODRONIA SERIATA

Triblidium seriatum Fries, Sclerom. Suec. *161.*
Dermatea seriata Tul. Fung. Carp. **3**: 160. 1865.
Gelatinosporium betulinum Peck, Ann. Rep. N. Y. State Mus. **25**: 84. 1873.

Apothecia occurring in elongated clumps 3–4 mm. long and about 2 mm. broad closely compressed together and often slightly irregular from mutual pressure, entirely black, reaching a diameter of .5 mm.; hymenium slightly concave, bordered by a slightly upturned margin, black; asci clavate, reaching a length of 95–110 μ and a diameter of 10–12 μ, 8-spored; spores long, fusiform and usually slightly curved when free, reaching a length of 45–60 μ and a diameter of 2–3 μ, 3-septate, paraphyses slender, branched, hyaline or subhyaline.

The conidial stage accompanies the ascigerous and consists of a blackish stroma in which the pycnospores are produced; pycnospores fusiform strongly curved and 3-septate, reaching a length of 40–45 μ from tip to tip and a diameter of 2–3 μ.

On *Betula lutea* and *Betula fontinalis.*

TYPE LOCALITY: Europe.

DISTRIBUTION: New York to Pennsylvania and Colorado; also in Europe.

EXSICCATI: N. Am. Fungi *537–537b;* Fungi Columb. *853;* Shear, N. Y. Fungi *200.*

A fine collection of this species was obtained in Coal Creek Canon, Colorado by the writer and Paul F. Shope in the summer of 1929 (No. *495*) and determined by Mr. W. W. Diehl as *Scleroderris seriata* (Fries) Rehm. This is the only perfect specimen of this species in the herbarium of The New York Botanical Garden from America.

Material which seems to be a part of the type collection of *Gelatinosporium betulinum* Peck is found in our collection. A note apparently in the handwriting of C. H. Peck reads as follows: "Perhaps the same as *Sphaeronema seriatum* B. & C. possibly a condition of *Cenangium seriatum* Fr." This conclusion is undoubtedly correct since our material collected in Colorado shows both stages on the same stroma. The pycnospores agree very closely with those from Peck's type. No definite pycnidia could be detected.

THE NEW YORK BOTANICAL GARDEN

DISTRIBUTION OF WEST INDIAN RUSTS

H. W. Thurston, Jr., and F. D. Kern

During the winter of 1931–32 while working with the rust flora of the Dominican Republic, we found it advantageous to prepare an index of all known species of West Indian rust fungi. Certain facts have become apparent from a study of this index that seem worthy of record and comment. Arthur (**2**) in 1917 gave a short collective account of the West Indian rusts as known at that time, in which he gave the total number of species as 214. Further study has resulted in reducing several of these to synonymy but further collecting in the Islands has added many new forms so that the present total is 290 species. Prior to the collecting of Stevens in Porto Rico 1913–15 it was the general impression of mycologists that rusts were scarce and uninteresting in these regions. As a result of Steven's work the total number of species was brought up to 155 (Arthur **1**, **2**). Arthur states that had a list been compiled before the Steven's material was available it would have numbered less than 100. Among previous collectors having a knowledge of the Uredinales were Clinton and Holway in Porto Rico and Earle in Cuba.

TABLE I

Tabular View of Rusts Known from West Indies at Various Times

Prior to 1915	1915	1916	1917	1932
100	155	174	214	290

Following Arthur's brief account in 1917, which included the Cuban list (**5**) although this list was not published until the following year, little systematic collecting was done in the Islands until 1924 and no papers of any extent dealing with the rusts of the region appeared until 1926. In 1926 Kern and Whetzel (**8**) added 12 species from Porto Rico; in 1928 Kern (**6**) added 13 from Santo Domingo; in 1930 Kern and Ciferri (**9**) 6 more from Santo Domingo; in 1932 Kern (**7**), and in 1933 Kern, Ciferri and

Thurston (**10**) added 28 from Porto Rico and Santo Domingo. Other collections from the Islands have been reported in different publications and most of these have also appeared in the various parts of the North American Flora (Vol. 7), bringing the total number of species as at present understood to 290 as already stated.

Arthur (**4**, p. 177) has well set forth the incompleteness of our knowledge regarding the distribution of rust fungi, and has discussed the cogent reasons for this state of affairs. No claim to completeness so far as distribution is concerned is made for the West Indian figures here presented. They represent merely an accounting which has not been attempted for this region for fifteen years. Using the figure 1200 as given by Arthur (**4**, p. 180) for the total number of the rusts of North America, in the West Indies are thus seen to occur between one fifth and one fourth of the known North American forms.

TABLE II

NUMBER OF WEST INDIAN RUSTS IN RELATION TO THEIR DISTRIBUTION ELSEWHERE IN THE WORLD

No. Known from West Indies Only	No. Known Also Only from Continental North America	No. Known Also Only from Continental South America	No. Known Also from Both North and South America	No. Known Also from Both Eastern and Western Hemispheres	No. Known Also Only from Eastern Hemisphere
71 or 24.1%	68 or 23.6%	50 or 17%	49 or 16.9%	43 or 15%	9 or 2.7%

By combining columns 1, 3, and 6 in Table II we find that there are 130 species from the West Indies not otherwise recorded in the flora of North America. Thus the Islands have contributed about one out of every 10 rusts known in North America. As a whole the rust flora of the Islands resembles that of North America only slightly more than that of South America. When the South American flora is better known this difference may change or disappear.

The distribution of the 290 species among the various islands of the West Indies is shown in Table III. This table reflects the extent and thoroughness of collecting in the individual islands rather than the real distribution. More time spent in collecting

and study of the less well represented areas will no doubt extend the records of distribution of a large number of species. The increase in our knowledge of West Indian rusts and their distribution is, however, strikingly apparent, and is here well illustrated by the figures from Santo Domingo, where the number of species known has increased from 4 in 1918 to 180 in 1932.

TABLE III

KNOWN DISTRIBUTION OF RUSTS IN THE VARIOUS ISLANDS OF THE WEST INDIES

Island	1918	1932	1932 No. Known Only from
Porto Rico	157 [1]	187	26
Santo Domingo	4 [2]	180	33
Cuba	136	162	32
Jamaica	32	72	8
St. Croix	7	28	1
Bahamas	12	27	7
St. Thomas	5	21	1
Haiti	3	17	
Martinique	5	14	
Guadaloupe	4	6	
Grenada	2	6	
Antigua	2	5	1
Tortola	1	4	1
Barbados	1	4	
St. Vincent	1	2	
Montserrat		2	
St. John		1	
Sinoloa		1	
St. Kitts		1	
Grand Caymon		1	

[1] Arthur, J. C. Myc. 9: 55–104. 1917.

[2] Arthur, J. C. & Johnston, J. R. Ured. of Cuba. Mem. Torr. Club 17: 97–175. 1918.

The 1918 distribution for all islands except Porto Rico is taken from this paper.

Organized collecting of rust fungi has been undertaken only in the three larger Islands and of these Porto Rico has probably been covered the most thoroughly. In presenting the Cuban list Arthur said, "it is evident that the present showing must be accepted as only a beginning." Incidental collecting in Cuba since that time, 1918, has increased the number of species from 136 to 162, which tends to bear out Arthur's statement. Jamaica never has been systematically searched for rusts, yet the number

of rusts known from Jamaica has gradually increased until it has more than doubled in the period under discussion.

It is of special interest to note the number of species which are known only from the type collections or type locality, 26 in Porto Rico, 33 in Santo Domingo, and 32 in Cuba. Undoubtedly only a few of these will eventually prove to be as rare as the present known distribution would indicate. Recent collections in Santo Domingo have uncovered six undescribed species. These facts are an indication that the West Indies are still one of the most fertile fields in North America for the rust specialist.

TABLE IV

DISTRIBUTION OF WEST INDIAN RUST SPECIES BY GENERA

	Total	W. I. Only		Total	W. I. Only
Aecidium	12	8	*Kuehneola*	1	
Alveolaria	1		*Milesia*	3	1
Botryorhiza	1	1	*Olivea*	2	1
Calliospora	1		*Phakopsora*	7	2
Cerotelium	4		*Prospodium*	7	3
Coleosporium	7		*Puccinia*	119	16
Cronartium	2	1	*Pucciniastrum*	1	
(includes *Cionothrix*)			*Pucciniosira*	1	
Crossopsora	2	1	*Ravenelia*	19	6
Clenoderma	1		*Sphaerophragmium*	1	
Desmella	1		*Thecopsora*	1	
Diabole	1	1	*Tranzschelia*	2	
Dicheirinia	1		(includes *Nephlyetis*)		
Endophylloides	1		*Uredo*	50	27
Endophyllum	3		*Uromyces*	37	3
Gymnosporangium	1		Total	290	71

Keeping in mind the impressions of the earlier mycologists that the rust flora of this region was uninteresting and lacked variety it is worthy of note that so many genera are now represented. When attention is given to the fact that 62 species or approximately 20 percent of the known West Indian rusts are now of necessity referred to the form genera *Aecidium* and *Uredo*, *Aecidium* with 12 and *Uredo* with 50 forms, the opportunity for studying not only the taxonomy, but the biology of the rusts in this region becomes apparent. In addition to the 50 *Uredo* forms, the other spore stages of which are totally unknown, there is a large proportion of the remaining species, Arthur (**2**) says 65 per cent, that habitually propagate in this region almost entirely by

means of urediniospores. No locality of equal area in North America offers a better opportunity to study the effects of environment upon life cycle, or possesses a larger number of imperfectly understood species which might be straightened out by culture methods, or by manipulation of host and environmental factors, to produce additional spore stages.

To promote further observations and investigations of the species now referred necessarily to the form genera *Aecidium* and *Uredo* we are presenting herewith a list which includes the host genera and the localities.

CHECK LIST OF WEST INDIAN RUST SPECIES REFERRED TO THE FORM GENERA AECIDIUM AND UREDO

A. AECIDIUM

1. *Aecidium abscedens* Arth., on *Randia:* Porto Rico, Santo Domingo.
2. *Aecidium Borreriae* Pat., on *Hemidiodia;* Porto Rico, Santo Domingo, Guadeloupe.
3. *Aecidium Bourreriae* Holw., on *Bourreria;* Bahamas.
4. *Aecidium Cordiae* P. Henn., on *Varronia;* Santo Domingo, Haiti.
5. *Aecidium domingensis* Kern & Cif., on *Baccharis;* Santo Domingo.
6. *Aecidium Farameae* Arth., on *Faramea:* Santo Domingo, Cuba.
7. *Aecidium favaceum* Arth., on *Phyllanthus;* Porto Rico, Santo Domingo.
8. *Aecidium hispaniolae* K. C. T., on *Solanum;* Santo Domingo.
9. *Aecidium Ixorae* Arth., on *Ixora;* Cuba.
10. *Aecidium Pisoniae* Arth. & Johnston, on *Pisonia;* Cuba.
11. *Aecidium simplicius* Arth. & Johnston, on *Tecoma;* Cuba.
12. *Aecidium Tournefortiae* P. Henn., on *Tournefortia;* Porto Rico, Santo Domingo, Cuba.

B. UREDO

1. *Uredo amicosa* Arth., on *Chrysophyllum;* Porto Rico.
2. *Uredo Anthurii* (Hariot) Sacc., on *Anthurium;* Porto Rico, Santo Domingo.
3. *Uredo Artocarpi* Berk. & Br., on *Artocarpus* & *Castilloa;* Porto Rico, Santo Domingo, Cuba.
4. *Uredo bauhiniicola* P. Henn., on *Bauhinia:* Cuba.
5. *Uredo Bixae* Arth., on *Bixa;* Porto Rico, Santo Domingo.
6. *Uredo Borreriae* (P. Henn.) Kern & Whetzel, on *Borreria;* Porto Rico.
7. *Uredo Buchenaviae* Kern & Whetzel, on *Buchenavia;* Porto Rico.
8. *Uredo bullula* Kern, on *Eupatorium;* Santo Domingo.
9. *Uredo Campeliae* Kern & Whetzel, on *Campelia;* Porto Rico.
10. *Uredo Cephalanthi* Arth., on *Cephalanthus;* Cuba.
11. *Uredo Chardoni* Kern, on *Bouteloua;* Porto Rico.
12. *Uredo Cherimoliae* Lagerh., on *Annona;* Cuba.
13. *Uredo Clusiae* Arth., on *Clusia;* Porto Rico.
14. *Uredo Coccolobae* P. Henn., on *Coccolobis;* Porto Rico, Cuba, Santo Domingo.

15. *Uredo cumula* Arth., on *Buchnera;* Cuba.
16. *Uredo Cupheae* P. Henn., on *Ginoria* & *Parsonsia;* Porto Rico, Santo Domingo, Jamaica, Cuba.
17. *Uredo curvata* Arth., on *Inga;* Cuba.
18. *Uredo dioscoreicola* K. C. T., on *Dioscorea* & *Rajania;* Porto Rico, Santo Domingo, Cuba.
19. *Uredo egenula* Arth., on *Sporobolus;* Jamaica, Santo Domingo.
20. *Uredo Eichorniae* Frag. & Cif., on *Eichornia;* Santo Domingo.
21. *Uredo Erythroxylonis* Graz., on *Erythroxylon;* Porto Rico, Cuba.
22. *Uredo Guacae* Mayor, on *Epidendrum* & *Spathiger;* Porto Rico, Santo Domingo.
23. *Uredo guaynabensis* Kern & Whetzel, on *Jussiaea;* Porto Rico, Jamaica, Cuba.
24. *Uredo Gynandrearum* Corda, on *Habenaria* & *Prescottia;* Porto Rico, Santo Domingo, Jamaica, Cuba.
25. *Uredo Hameliae* Arth., on *Hamelia;* Porto Rico, Santo Domingo.
26. *Uredo Hymenaeae* Mayor, on *Hymenaea;* Porto Rico, Santo Domingo, Cuba.
27. *Uredo ignava* Arth., on *Bambos;* Porto Rico, Santo Domingo, Jamaica, Cuba.
28. *Uredo incomposita* Kern, on *Eleocharis;* Porto Rico, Santo Domingo.
29. *Uredo jatrophicola* Arth., on *Adenoropium* & *Curcas;* Porto Rico, Santo Domingo, St. Croix, Cuba.
30. *Uredo Kyllingae* P. Henn., on *Kyllinga;* Porto Rico, Santo Domingo.
31. *Uredo laeticolor* Arth., on *Operculina;* Porto Rico, Cuba.
32. *Uredo Lucumae* Arth. & Johnston, on *Lucuma;* Cuba.
33. *Uredo lutea* Arth., on *Chamaefistula;* Porto Rico.
34. *Uredo nigropuncta* P. Henn., on *Bletia;* Porto Rico, Santo Domingo, Haiti, Bahamas, Cuba.
35. *Uredo Ornithidii* K. C. T., on *Ornithidium;* Santo Domingo.
36. *Uredo Polytaenii* K. C. T., on *Polytaenium;* Porto Rico, Santo Domingo.
37. *Uredo Piperis* P. Henn., on *Peperomia;* Porto Rico.
38. *Uredo pustulata* P. Henn., on *Stenorrhynchus;* Porto Rico.
39. *Uredo Rousseliae* Kern & Whetzel, on *Rousselia;* Porto Rico.
40. *Uredo rubescens* Arth., on *Dorstenia;* Porto Rico, Santo Domingo.
41. *Uredo sabiceicola* Arth., on *Sabicea;* Porto Rico.
42. *Uredo Sapotae* Arth. & Johnston, on *Sapota;* Santo Domingo, Bahamas, Cuba.
43. *Uredo Sauvagesiae* Arth., on *Sauvagesia;* Porto Rico.
44. *Uredo Saviae* Arth. & Johnston, on *Savia;* Cuba.
45. *Uredo Sparganophori* P. Henn., on *Struchium;* Porto Rico, Santo Domingo, Jamaica, Cuba.
46. *Uredo Toroiana* Kern, on *Vernonia;* Santo Domingo, Haiti.
47. *Uredo Trichiliae* Arth., on *Trichilia;* Porto Rico.
48. *Uredo uncinata* K. C. T., on *Dorstenia;* Porto Rico, Santo Domingo.
49. *Uredo vicina* Arth., on *Wedelia;* Porto Rico.
50. *Uredo Wilsoni* Arth., on *Anastraphia;* Bahamas.

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NOTES AND BRIEF ARTICLES

Beginning with the present number, the dates of publication of Mycologia will be: February 1st, April 1st, June 1st, August 1st, October 1st, and December 1st, instead of January 1st, March 1st, May 1st, July 1st, September 1st, and November 1st. This arrangement will allow more leeway in the publication of the first and last issues containing, respectively, the report of the annual meeting of the Mycological Society of America and the volume index.

Faull's Monograph of the Genus Milesia [1]

A notable and more than usually important addition to the literature of the Uredinales is embodied in this comprehensive treatise of the most unique and least understood genus of all the rusts. In taxonomic treatment it evaluates each historical reference both as to genus and species, and for geographical distribution embraces all known material throughout the world.

The genus is one of the two white-spored genera of rusts inhabiting ferns, and is here adequately described for the first time. The urediospores are a predominating feature, although teliospores are not uncommon and were present but overlooked in the establishment of the genus. Both telia and aecia, the latter on *Abies*, may afford some taxonomic aid, but are less important in this respect than the urediospores. The key to species is based wholly upon uredinial characters and is illustrated with figures of urediospores drawn to a uniform scale. Thirty-three species and two varieties are described, thirteen as new, of which the aecia are known for nine species, and the telia for twenty-four species and varieties. Most of the species are best collected on the over-wintered fronds.

In selecting the generic name to accord with the present International Rules of Nomenclature it is pointed out that two

[1] Faull, Joseph Horace. Taxonomy and geographical distribution of the genus *Milesia*. Contr. Arnold Arboretum, Harvard Univ. II. 138 pp., 9 pl. 1932.

interpretations may be placed on Rule 49 *bis*. Either the "perfect state," which is made the essential basis for an acceptable name, may refer to the haploid stage in which both uredia and telia are produced from the same mycelium, and which are therefore not comparable to conidia and asci in the Ascomycetes, or, judging from the examples appended, the "perfect state" may refer to the telia and teliospores alone.

The author relies upon the first interpretation in selecting the generic name *Milesia* and is led to anticipate that the Rules will eventually be emended to remove the ambiguity. Those who are interested in the validity of names originally based in part or wholly on uredinial characters will find in the first few pages of the monograph an unbiased and judicial statement of the controversy pertaining to the value of "uredo names," as illustrated by the genus *Milesia*.

J. C. ARTHUR.

The Mycological Society of America

The Mycological Society of America held its first annual meeting December 28, 29, and 30 in the Hotel Traymore at Atlantic City, New Jersey, in affiliation with the American Association for the Advancement of Science. The sessions were well attended, and the meeting as a whole was outstandingly successful. Forty papers illustrating a wide and varied interest within the general field of mycology were presented. Papers on Phycomycetes and on aspects of sexuality in Ascomycetes and rusts were especially numerous. The Society held a joint session with Section G and another with the American Phytopathological Society.

At the foundation of the Society the preceding December in New Orleans an organizing committee of five members had been named. This committee, composed of president Wm. H. Weston, Jr., secretary-treasurer H. M. Fitzpatrick, and councilors H. S. Jackson, C. R. Orton, and N. E. Stevens, gave consideration during the year to the problems confronting the Society, and sent out an invitation to charter membership to mycologists in general which brought forth a very gratifying response. At Atlantic City in an open business session under the chairmanship of president Weston the Society completed its organization. A con-

stitution and by-laws were adopted. The journal MYCOLOGIA became the official organ of the Society on terms previously arranged with The New York Botanical Garden, and the following officers and editors were elected.

OFFICERS

C. L. Shear.....*President*
G. W. Martin.....*Vice-president*
H. M. Fitzpatrick.....*Secretary-treasurer*
H. S. Jackson.....*Councilor*
C. R. Orton.....*Councilor*

EDITORIAL BOARD

F. J. Seaver, *Editor-in-chief*
G. R. Bisby
H. M. Fitzpatrick
E. B. Mains
J. A. Stevenson
F. A. Wolf

The editorial board elects its editor-in-chief annually. For 1933 it chose F. J. Seaver, who has also been designated by The New York Botanical Garden as managing-editor.

The vice-president was empowered to arrange for a summer meeting at such time and place as he shall select. It is expected that this meeting will be primarily of the nature of a foray. The hope has been expressed in various quarters that the importance of this annual get-together in the field will be generally recognized, and that all will coöperate in making it a complete success.

The Society begins its active existence with a charter membership of approximately three hundred and fifteen. It is expected that this number will be increased appreciably during the coming year. All persons interested in the fungi are eligible to membership. The annual dues of five dollars entitles the member to receive MYCOLOGIA. Applications for membership should be addressed to the secretary-treasurer. A group photograph of the mycologists was taken at one of the sessions in Atlantic City. A key to this is available.

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